PATTERNS OF RESOURCE USE WITHIN THE BROWSING RUMINANT GUILD IN THE CENTRAL KRUGER NATIONAL PARK

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ABSTRACT

The use of habitats and food by giraffe, kudu, impala, and steenbok was studied during 11 months of fieldwork, divided in the central region of the Kruger National Park, South Africa. This was to identify mechanisms of resource partitioning among browsers, and to investigate browser-plant interactions. Vegetation was typical savanna on a basaltic plain, and granite hills. The wet season was the dry season. Resource was used to estimate home range areas and to test habitat selection. 1,094 observations of diurnal activity, and observations of feeding time were recorded using a handheld dictaphone.

Average home range areas were: giraffe, 282 km²; kudu, 21 km²; impala, 7.61 km²; steenbok, 0.82 km². Home range area varied with body mass in proportion to $M^{0.75}$. Giraffe fed on a wide range of habitats (vegetation communities), whose diversity of habitat use was found to increase with decreasing body size. Steenbok remained in the upper strata throughout the year, but giraffe, kudu and impala converged on habitats of the lower strata during the dry season. Despite overlaps in habitat use, sympatric species fed along qualitatively different foraging paths.

Giraffe fed almost exclusively on foliage, pods and flowers of woody plants. The kudu diet was ± 35% forbs and creepers, and the rest woody browse. Impala mainly grazed during the wet season, but ± 50% of the dry season diet was forbs and woody browse. Steenbok fed mainly on forbs, and also woody browse and *Acacia* pods in the dry season. Mean dietary diversity and dietary overlap among the 4 browsers increased to a peak in the late dry season. Feeding preferences of kudu, impala and steenbok were negatively related to leaf condensed tannin values in the wet season. No such relationship was found for giraffe. Levels of condensed tannin were low, and leaf nitrogen high, in browse trees that had been severely browsed. A model is presented to explain this, and ecological implications of concentrate selective browsing are discussed.

Among the 4 species studied, resource partitioning is most clear-cut in the dry season, when abundance and quality of browse is low. Giraffe and kudu share preferences for certain tree species, while impala and steenbok prefer shrubs. Giraffe feed at a higher level than kudu, and impala feed along riverlines while steenbok keep to the upper catena. The importance of body size differences on ecological separation within the browsing ruminant guild is discussed.

DECLARATION

I declare that this thesis is my own work, and assistance from others was limited to that acknowledged in the preface. It is being submitted for the degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other university.

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PREFACE

Current understanding of the feeding ecology of African savanna ungulates stems largely from studies on the East African grazing guild. Although many single-species studies have been conducted before on browsers, this thesis represents the first study of an African savanna browsing ungulate guild. The thesis has four main purposes.

Firstly, it investigates how browsers that differ widely in body size respond to spatial and temporal heterogeneity in the savanna environment. Secondly, it investigates how feeding patterns differ among species, and factors responsible for such differences. Thirdly, it investigates interactions between browsers and their woody food plants. Fourthly, it considers the potential for interspecific interactions within the browsing ruminant guild. A dominant theme is the influence of body size on resource use. Comparisons are made throughout between patterns of resource use identified among browsers, and those previously described for grazers.

An overview of the influences of seasonality on the feeding patterns of browsers has been published (du Toit, 1987) in the proceedings of the Second

International Symposium on the Nutrition of Herbivores, held at the University of Queensland, Brisbane, in July 1987. A paper on the influence of body size on diversity of habitat use (du Toit and Owen-Smith, in press) has been accepted for publication in *The American Naturalist*.

I consider myself privileged to have had the opportunity of living and studying in the Kruger National Park. For this I am indebted to my supervisor, Dr. Norman Owen-Smith, who performed all the initial arrangements that made the project possible. I am also greatly indebted to the research section at Skukuza, who accepted me as an unknown quantity and provided all the facilities and assistance I required. Dr. S.C.J. Joubert, the present Park Warden, was particularly helpful in this regard.

Pat Wolff, Senior Ranger in charge of Tshokwane section, was a valuable source of help and advice throughout. Pat, Deneene, and their children also provided much valued friendship and hospitality to myself and my wife, Maryjane. A vital asset to this study was Peter Retief, Quantitative Biologist at Skukuza, who wrote the software for the data capture system I employed. Peter also assisted by solving all manner of data management problems with superb skill and utmost patience. Technical assistance was provided

by Andre Potgieter, Chief Research Technician at Skukuza, who could not have been more helpful. Oom Gert van Rooyen built the vehicle-mounted radio tracking antenna that proved invaluable in the field. Veterinary expertise, required in the immobilisation of animals for attaching radio collars, was provided by Dr. V. de Vos, Assistant Head of Research, and Ben de Klerk, Senior Technician. All the other scientists at Skukuza contributed with discussions, advice and hospitality, for which I am most grateful.

Dr. John Bryant, Associate Professor at the Institute of Arctic Biology, University of Alaska, was most generous in performing chemical analyses of leaf and soil samples. He also contributed with stimulating discussions in the field, and provided much advice in interpreting results of the analyses.

Financial support for the project was generously provided by the Foundation for Research Development of the Council for Scientific and Industrial Research, the South African Nature Foundation, the National Parks Board of South Africa, and the University of the Witwatersrand. The Endangered Wildlife Trust provided materials for radio transmitters at cost price, and these were assembled without charge (and very well) by Mr. Derek Ritchie of that organization.

At the University of the Witwatersrand, Dr. Norman Owen-Smith was an assiduous supervisor and I benefited greatly from his breadth of knowledge and the high academic standard he maintains. Professor Mike Mentis and his predecessor, Professor Brian Walker, provided valuable advice during degree committee meetings. Mrs. Liz Sole was extremely efficient and considerate in handling administrative matters.

My parents, Fred and Flo du Toit, were always ready to help. Both assisted by digitizing the home range data, and used computer graphics to produce maps of the study area. Flo du toit proof-read most of the manuscript. Finally my wife, Maryjane, assisted with vegetation measurements in the field, proof-reading, typing references, and many other aspects too numerous to mention but which are all very much appreciated.

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CHAPTER 1

INTRODUCTION

1.1 Why study African savanna browsers?

In comparison with the wealth of studies on the grass layer in southern African savanna ecosystems (reviewed by O'Connor, 1985), the browse component has received scant attention. The same has been said for East African savannas (Pellew, 1983b), where there has been a concentration of research effort on grasslands of the Serengeti ecosystem (reviewed in Sinclair and Norton-Griffiths, 1979). There is a requirement to redress this imbalance. Firstly, the subsistence economy of Africa is based largely on grazers (cattle), and continual overstocking has severely reduced the ability of grasslands to provide for a burgeoning human population. To alleviate this problem, development planners now recognize a need for research into the use of browse by indigenous ungulates, with a view towards management for meat production (Le Houerou, 1982; Kay, 1987). Secondly, without a sound understanding of all the components of an ecosystem, we can only resort to "cautious fiddling" in the management of that ecosystem (Walker and Goodman, 1983). This study is intended as a contribution towards developing a sounder understanding of the browser component of southern African savannas. It concerns the use of browse as a food resource by indigenous ruminants in the Kruger National Park (KNP), South Africa, with an emphasis on the mechanisms of resource partitioning.

1.2 Resource partitioning among African savanna ungulates

Large mammalian herbivores (>5 kg) of African savannas number some 44 species from 29 genera (Owen-Smith, 1982). Of these, over 20 species occur within the KNP (Pienaar, 1963). Lamprey (1963) advanced the first hypotheses explaining how such a diversity of large herbivore species may share the food resources of one ecosystem. Based on his studies in the Tarangire Game Reserve, Tanganyika (now Tanzania), Lamprey proposed that different species feed (a) in different habitats during the same season, or else in the same habitat during different seasons; (b) on different foods; and (c) at different levels in the vegetation. Although Lamprey did not employ rigorous statistical tests, his conclusions remain undisputed (McNaughton and Georgiadis, 1986). Ferrar and Walker (1974) employed discriminant function analysis in a detailed investigation into herbivore/habitat relationships in Kyle National Park, Rhodesia (now Zimbabwe). They found that large herbivore species differed with respect to the proportions of herbs, trees, and particularly shrubs, that contributed to total plant biomass at feeding sites used by each species. These differences were attributed to differences in preferred diets.

McNaughton and Georgiadis (1986) used correspondence

analysis to re-examine Lamprey's data and confirmed that syntopic large herbivores differ in their feeding preferences, with preference for either grass or browse being an important feature of resource partitioning. At the grazer end of the grazer-to-browser continuum (as termed by McNaughton and Georgiadis), it has been found that different species tend to select different plant parts (leaf, sheath and stem) from the sward (Gwynne and Bell, 1968; Bell, 1971). Ingesta of the larger grazers includes a relatively large proportion of stem, while that of the smaller grazers includes a relatively large proportion of leaf. These parts differ in fibre content (leaf lowest and stem highest) and hence *digestibility (van Soest, 1982). Larger herbivores are* able to tolerate a lower quality diet because of the allometric relationship between gut capacity and metabolic rate (Bell, 1971; Jarman, 1974; Demment and van Soest, 1985). By this relationship larger herbivores (a) retain food in the gut for longer, which promotes digestion efficiency; and (b) have lower mass-specific metabolic costs, so although they require a larger quantity of food (being larger-bodied) they can tolerate food of lower quality than smaller species can. All herbivores prefer a high quality diet (Bell, 1971) but because high quality food items are rare, large herbivores cannot harvest enough of them to live on and so usually feed on lower quality, more abundant foods (Bell, 1971; Jarman, 1974; Geist, 1974). Hence

body size differences among syntopic ungulates may result in available food being partitioned according to its nutritional quality (McNaughton and Georgiadis, 1986).

For ungulates, nutritional quality of grass tissue is determined largely by what Bell (1982) termed the M/C ratio (metabolite/cell wall ratio), or the ratio of proteins and soluble carbohydrates to structural carbohydrates (see also Bell, 1971; Janis, 1976; Owen-Smith, 1982; Demment and van Soest, 1985). In contrast with grasses, the tritional quality of dicotyledonous forage types (browse) is influenced not only by structural carbohydrates, but also secondary defence compounds (Freeland and Janzen, 1974; Rosenthal and Janzen, 1979; Bryant and Kuropat, 1980; Cooper and Owen-Smith, 1986; Malechek and Balph, 1987; Cooper *et al.*, 1988). Tolerance of these compounds by differently-sized African ungulates has not yet been investigated in the way that tolerance for fibre has.

1.3 Hypotheses

Summarizing the above, resource partitioning among coexisting ungulates in any particular African savanna ecosystem is presently understood in terms of the following hypotheses:

1). Ungulate species separate spatially and temporally by feeding in different habitats (plant communities) during the same season, or in the same habitat but during different seasons (Lamprey, 1963).

2). Syntopic ungulate species include different proportions of grass and browse in their diets (Lamprey, 1963; McNaughton and Georgiadis, 1986).

3). Differently-sized ungulate species select diets that differ with respect to nutritional quality (Gwynne and Bell, 1968; Bell, 1971; Jarman, 1974; Geist, 1974; Demment and van Soest, 1985; McNaughton and Georgiadis, 1986).

4). Differently-sized browsing ungulate species feed at different levels in the vegetation (Lamprey, 1963).

These hypotheses reflect the common tendency for animal species in trophically similar groups to partition their food resources by feeding in separate habitats and, where habitat uses overlap, by adopting different feeding patterns (Schoener, 1974a, 1986a). Here I test the above hypotheses by addressing the following questions concerning the seasonal use of space and food by coexisting browsing ruminant species:

1.4 Questions

1). Which habitats (plant communities) does each species use and when are they used?

2). How do their habitat preferences differ, and what are the reasons for such differences?

3). What spectrum of food resources does each species use and when are they used?

4). How do their feeding preferences differ, and what are the reasons for such differences?

The approach I adopt in answering these questions emphasises the influence of body size differences on resource-use differences among species. Body size determines dietary tolerance, and hence the range of food quantity and quality used, which is a key factor in the feeding ecology of large herbivores (Bell, 1971, 1984). The above four questions concern the influences of distribution, abundance, and chemical composition of plants on the distribution and feeding patterns of large herbivores. However, timing, intensity, selectivity and spatial patterning of herbivory may also influence the establishment, growth, chemical composition, and seed set of plants (Crawley, 1983).

Hence I address a fifth question concerning the interaction between browsers and woody plants, i.e.:

5). How do browsing ruminants influence the palatability and abundance of their woody food plants?

1.5 The guild

A trophically similar group of species is termed a *guild*, originally defined by Root (1967:335) as a group of "species that exploit the same class of environmental resources in a similar way." The guild concept is gaining popularity in community ecology as a functional means of classifying species by exploitation pattern rather than taxon (reviewed by Terborgh and Robinson, 1986). For example a guild study of desert granivores in North America investigated competitive interactions among rodents, birds and ants (Brown *et al.*, 1986). However, despite its attributes, this multi-taxon approach is seldom adopted. In the case of the "savanna folivore guild" such an approach would require the expertise and facilities to study a vast range of animal species, from insects and gastropods to birds and mammals. Hence it is more usual that limitations of time, methodology, and breadth of expertise restrict guild studies to taxonomically related species that exploit the same class of

resources in a similar manner (Jaksic, 1981; Schoener 1986*b*; Terborgh and Robinson, 1986). Here I have restricted the study to savanna ruminants that depend to a large degree on dicotyledonous plants for their food. Non-ruminant species that also depend on the browse resource [i.e. black rhinoceros (*Diceros bicornis*) and elephant (*Loxodonta africana*)] were not studied because the present population of black rhinoceros in the KNP is very small (± 140 individuals), and an ongoing study of elephant ecology is being conducted by the KNP research staff (Hall-Martin, 1986).

I apply the term "browsing" to feeding off dicotyledonous plants, both herbaceous and woody (*sensu* Owen-Smith, 1982; but see Hofmann and Stewart, 1972). To the savanna ruminant, foliage of these plants (browse) differs from that of monocotyledons (grasses) in a number of ways (reviewed by Owen-Smith, 1982; Malechek and Balph, 1987). Firstly, browse generally contains higher levels of crude protein, but also higher levels of secondary defence compounds, than grass does. Secondly, the physical presentation of leaf and stem on browse plants requires adaptations in feeding behaviour and feeding apparatus (e.g. muzzle width and dentition) that distinguish browsers and mixed feeders from grazers. Furthermore, Hofmann and Stewart (1972) found differences in stomach structure

that separate grazers from browsers and mixed feeders (although they did not use these terms), presumably due to digestion-related differences between browse and grass (e.g. different fermentation rates). Hence browse and grass constitute two distinct food resource types, and so two distinct guilds may be identified among the ruminants that use them. Note, however, that the guild is defined in terms of a class of resources (Root, 1967) which are in turn defined by the investigator (Jaksic, 1981), so a mixed feeder could be included in a grazing guild or a browsing guild depending on the resource class by which the guild is defined.

Due to reasons of time and logistics, this study does not include all savanna browsing ruminants. However, the species it does include were selected firstly because they are the most common browsers in the study area (Pienaar, 1963), and secondly because they effectively represent the full range of extant ruminant body sizes. These species are as follows (nomenclature and data from Smithers, 1983):

1). Giraffe [*Giraffa camelopardalis* (Linnaeus, 1758)]. The tallest of all animals and the heaviest ruminant. Mean body mass: (F) 830 kg; (M) 1,200 kg. Occur from the eastern Transvaal in South Africa to Somalia and West Africa. Purely browsers, gregarious.

2). Kudu [*Tragelaphus strepsiceros* (Pallas, 1766)]. Mean body mass: (F) 160 kg; (M) 230 kg. Occur from Sudan to the Cape. Predominantly browsers, gregarious.

3). Impala [*Aepyceros melampus melampus* (Lichtenstein, 1812)]. Mean body mass: (F) 41 kg; (M) 54 kg. Occur from northern Kenya to northern Natal, South Africa. Mixed feeders (browse and graze), gregarious.

4). Steenbok [*Raphicerus campestris* (Thunberg, 1811)]. One of the smallest savanna ruminant species. Mean body mass (both sexes): 11 kg. Occur in two discrete areas; East Africa and southern Africa. Predominantly browsers, although apparently mixed feeders in some areas. Solitary.

1.6 Intraguild relations

The question generally asked in guild studies is how species partition the resources of a given habitat (Terborgh and Robinson, 1986). Why it is that resource partitioning occurs is a subject of recent debate. The currently dominant hypothesis is that where differences among species (e.g. morphological) are sufficient to result in resource partitioning, such differences are the result of past or present pressures to avoid

interspecific competition within the guild (discussed by Schoener, 1986a). The opposing (null) hypothesis is that similar differences would be found if the same number of species was drawn at random from a larger species pool (Strong *et al.*, 1979; Simberloff, 1983). The competition hypothesis stems from the early mathematical theories and laboratory experiments of Lotka, Volterra and Gause (see Krebs, 1985), expressed in Gause's principle: two species with identical ecological niches cannot coexist in nature. Strictly speaking this is paradoxical as different species cannot have identical ecological niches (Cole, 1960), but what is meant is that species cannot coexist for long if their resource use patterns are too similar.

The assumption that guild members compete for shared resources has lead to ambiguity over whether a guild should be defined in terms of (a) resources used or (b) competition for those resources (discussed by MacNally, 1983). Hairston (1981:70) has stated his view that a guild is "a product of the imagination" unless evidence of competition can be found. Such an approach overlooks the possibility that present-day competition is prevented by the "ghost of competition past", the results of competition over evolutionary time (Schroder and Rosenzweig, 1975; MacNally, 1983; but see Connell, 1980). It also overlooks the possibility that predation regulates populations within the guild so that the

potential for competition is not realised (Connell, 1975). Furthermore, the presence or absence of competition among consumer species may have little bearing on the effects of consumption on the resource itself. Whether a food item is eaten by species A or species B does not alter the fact that it is eaten, and whether A and B are competitors or not does not alter the fact that if they both use the same class of resources in a similar way then they belong to the same guild (Jaksic, 1981; MacMahon *et al.*, 1981). Finally by Root's (1967) definition, there is no requirement that competition be demonstrated as a prerequisite to the use of the guild concept (see also Terborgh and Robinson, 1986).

Assessing the significance of interspecific competition to guild structure is problematic, requiring perturbation experiments (Schoener, 1974a; MacNally, 1983). Such experiments are usually impossible to perform with natural populations of large herbivores, for which the presence or absence of interspecific competition has to be gauged by inferrence (Sinclair and Norton-Griffiths, 1982; Sinclair, 1985; McNaughton and Georgiadis, 1986). Hence this study does not hope to test competition theory. Rather, it is a comparative analysis of resource use among members of a herbivore guild. An observation-based approach such as this constitutes the groundwork required for reaching the

first step in understanding constraints on resource use by species within a particular community or ecosystem (Moermond, 1986). Subsequent steps entail refinement of this understanding by testing specific hypotheses by experimentation (see Mentis, 1988). This thesis is intended as a contribution towards reaching the first step in the process for browsing ruminants in the central KNP.

CHAPTER 2

STUDY AREA

2.1 Location and duration of field work

Fieldwork was conducted in the Tshokwane section of the central KNP (Fig.2.1), with the centre of the study area being Nwamuriwa Hill (Fig. 2.2), near the Tshokwane ranger station (24°47'S, 31°52'E). Exploratory fieldwork commenced in May 1984. Data capture commenced in July 1984 for locational data, and September 1984 for feeding data. Fieldwork was terminated at the end of December 1986. The extent of the study area depended on the movement of study animals, but the area within which most data were collected was approximately 160 km^2.

2.2 Geomorphology

The elongate shape of the KNP (± 320 km x 66 km), oriented north/south on the upper Moçambique coastal plain, results in the Park being characterised by parallel geological formations. These stretch the length of the Park, with mainly granitic formations on the western half and basalts in the east. The two formations are divided y a narrow belt of Karoo sediments (shale and sandstone). This belt formed the western edge of the study area, with the Lebombo Hills on the eastern edge along the border with Moçambique. The Lebombo Hills are composed of rhyolite, and the adjoining Nwamuriwa, Nwamuriwane, and Nkumbe hills are

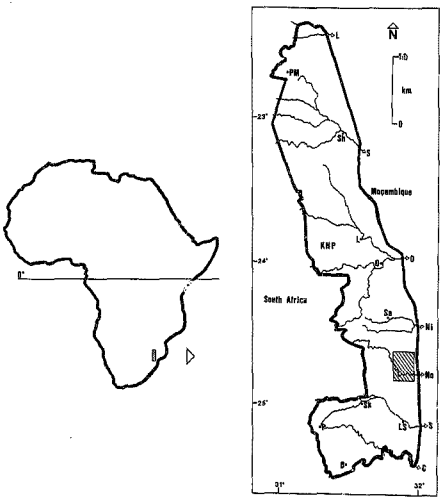

Figure 2.1. Position of the Kruger National Park (KNP) within the African continent, and the study area (shaded) within the KNP. Camps: B, Berg-en-dal; C, Crocodile Bridge; P, Pretorius Kop; LS, Lower . .bie; Sk, Skukuza (Park Headquarters); Se, Satara; O, Olifants; L, Letaba; Sh, Shingwedzi; PM, Punda Maria. Major rivers: C, Crocodile; S, Sabie; Nw, Nwaswitsontso; Ni, Nwanedzi; O, Olifants; S, Shingwedzi; L, Levhuvhu/Limpopo.

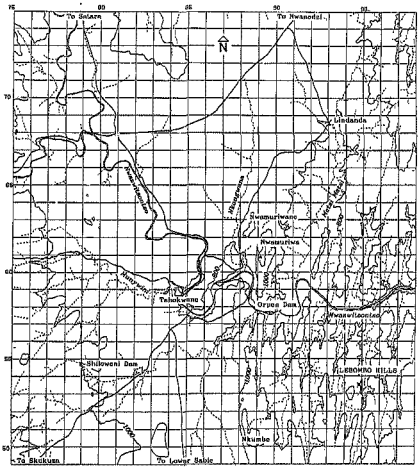

Figure 2.2. The Tshokwane study area, centred on Nwamuriwa Hill. Scale: each grid square represents 1 km², Contour interval: 200 English feet (61 m).

composed of granophyre (Schutte, 1986). Between the Karoo sediments and the Lebombo Hills is an undulating plain of basaltic clays. Tshokwane ranger station is 245 m above sea level.

Major rivers draining the KNP flow from the Transvaal highveld in the west to the Indian Ocean in the east. The Nwaswitsontso River, which drains the Tshokwane section, is seasonal although many pools persist throughout the year. Tributaries such as the Metsi Metsi and Munywini only flow for short periods after good rains.

2.3 Climate

Mean annual rainfall at Tshokwane from 1975/76-1985/86 was 592 mm. The mean over the 20-year wet/dry cycle from 1959/60-1978/79 was 531 mm, with 84% of this during the 6 months from October to March (data from Gertenbach, 1980). Since this area receives under 650 mm rainfall per year, it may be classified as a semi-arid savanna (see Huntley, 1982). Rainfall during the study period (Fig. 2.3) was relatively high during 1984/85 (809 mm) and low during 1985/86 (439 mm). Monthly rainfall totals for July 1984 and February 1985 were particularly high (relative to the averages for those months), while monthly totals for December 1985 to February 1986 were particularly low.

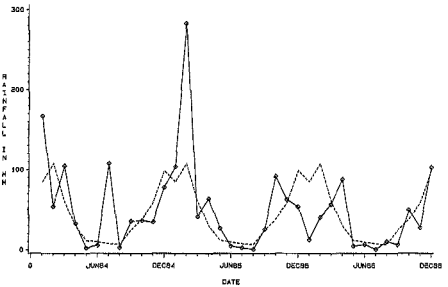

Figure 2.3. Monthly rainfall totals (mm) at Tshokwane during the study period (solid line), and mean monthly rainfall for Tshokwane over one 20-year wet/dry cycle, from 1959/60 to 1978/79 (dashed line).

Average daily maximum temperature (using data for Skukuza, collected since 1965; in Gertenbach, 1983) is at its highest between November and March (± 32°C), with temperatures reaching up to 44°C. Lowest average daily minimum is in June/July (± 6°C). Frost is uncommon.

2.4 Vegetation

The vegetation of the central KNP has been described in detail by Coetzee (1983) and Gertenbach (1983). The two main landscapes in the study area are the Lebombo South and *Sclerocarya birrea/Acacia nigrescens* savanna landscapes (Gertenbach, 1983). The Lebombo South landscape occurs along the eastern edge of the study area, in the Lebombo Hills. Here the shrubby woody layer on thin and rocky soils is dominated by *Combretum apiculatum* and *Pterocarpus rotundifolius*. The grasses *Themeda triandra* and *Digitaria eriantha* dominate the herb layer. *Sclerocarya birrea/Acacia nigrescens* savanna occurs on basaltic clays, and is an open tree savanna with a generally dense herb layer dominated by grasses (*Themeda triandra* and *Bothriochloa radicans* are common). The vegetation communities (habitats) within these landscapes are described in Chapter 3.

The seasonal rainfall pattern in the KNP causes profound seasonal changes in the savanna vegetation.

These changes are not uniform across the landscape, however, due to soil moisture variations across the catenary drainage sequence. Most woody plants on the upper catena are deciduous, while many of those growing along watercourses and riverlines are evergreen. Hence the drainage lines are clearly defined in the dry season as threads of green vegetation against a bare, brown background.

The abundance and distribution of forbs in the central KNP is dependent upon both soil moisture and grass cover. In the study area, forbs are more abundant along the Nwamuriwa/Nwamuriwane hillbase, and along drainage lines, than in the *Sclerocarya birrea/Acacia nigrescens* savanna (personal records, and see Novellie, 1983). Forbs are also locally abundant in patches where the grass layer has been weakened by severe grazing, such as near seasonal waterholes on the upper catena (personal records). Where the grass cover is dense, most dicotyledonous herbs are creepers (e.g. *Cucumis*, *Turbina* and *Ipomoea* spp.), which entwine among the grass tufts.

The KNP has had a burning programme for the last 40 years, and the current programme is aimed at simulating the natural fire regime. Burning is done within specific areas selected on the basis of previous fires (e.g. lightning-induced) and rainfall (Joubert, 1986).

Burning occurred in patches within the study area during the study period, but the complete area was never burnt at one time.

2.5 Fauna

The most common large herbivore species in the Tshokwane area are wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*). These species become particularly abundant in the wet season, and migrate southwards in the dry season. Buffalo (*Syncerus caffer*) and elephant (*Loxodonta africana*) are also common, although elephant are mainly represented by lone bulls or bachelor groups. Impala are very common, especially in the loop of the Nwaswitsontso River at Tshokwane. Other common species include giraffe, kudu, waterbuck (*Kobus ellipsiprymnus*), warthog (*Phacochoerus aethiopicus*), steenbok and ostrich (*Struthio camelus*). Bushbuck (*Tragelaphus scriptus*) and duiker (*Sylvicapra grimmia*) occur in riverine thickets of the Nwaswitsontso River, and klipspringer (*Oreotragus oreotragus*) are common on Nwamuriwa, Nwamuriwane, and Nkumbe hills. Hippopotamus (*Hippopotamus amphibius*) occur in the vicinity of pools in the Nwaswitsontso River, and Shiloweni Dam. Less common large herbivores include white rhinoceros (*Ceratotherium simum*), black rhinoceros (*Diceros bicornis*), tsessebe (*Damaliscus lunatus*), sable (*Hippotragus niger*), and reedbuck

(*Redunca arundinum*). One eland cow (*Taurotragus oryx*) was sighted in the study area once.

The large predator guild consists mainly of lion (*Panthera leo*), spotted hyaena (*Crocuta crocuta*), and leopard (*Panthera pardus*). Cheetah (*Acinonyx jubatus*) and wild dog (*Lycaon pictus*) are not common but relatively well represented in the Tshokwane area.

Populations of elephant, buffalo and hippopotamus are carefully monitored and controlled by culling (de Vos *et al.*, 1983). No other species are culled, although wildebeest, zebra and impala have been culled in the past. Movement of animals across the Park boundaries is restricted by fencing (erected during the 1960s and 1970s), mainly for veterinary reasons. Subpopulations of migratory species (wildebeest and zebra) have adapted to new migration routes within the Park, which covers 19,485 km^2. Hence the KNP is a large and carefully conserved natural ecosystem that provides ideal opportunities for ecological research. Fears expressed by McNaughton and Georgiadis (1986) that data from the KNP are unreliable due to over-management are, I believe, quite unfounded. Management strategies employed in the KNP, and the methods used to monitor them, are documented (e.g. de Vos *et al.*, 1983; Joubert, 1983; Pienaar, 1983) so that outside

researchers may independently evaluate their effects on the KNP ecosystem.

CHAPTER 3

SPATIAL PATTERNS OF RESOURCE USE

3.1 INTRODUCTION

This chapter is concerned with the distribution of browsing ruminants across a savanna landscape, and factors that might be responsible for the observed pattern.

An individual of any one species is adapted to a subset of biotic and abiotic factors in its environment so that it may live and reproduce. The "biotope" has been revived by Goodall (1986:30) as a label for this part of the environment, which is defined as *"a particular region of space and time within one or more ecosystems, in which an individual of that species may be able to establish itself and complete its life cycle."* This definition constitutes a connection between "niche" and "habitat" by extracting the spatial and temporal dimensions from the n-dimensional niche for a species and placing them in the biotope, which is a conceptual overlay upon the habitat distribution pattern for a geographical area. Goodall's biotope concept has a particularly useful application to the browsing ruminant guild of the central KNP, which includes species that make use of more than one habitat with intensities that vary between seasons. Here attention is focused on the factors responsible for differences between biotopes, with particular reference to differences in body size and habitat selection.

3.1.1 Body size and habitat specialisation

Large species generally occur at lower population densities than small species but, being larger, use more energy per individual. The balance between population density and energy use per individual determines how evenly community resources are shared among differently sized species. Brown and Maurer (1986) have shown that in communities of North American birds, granivorous desert rodents, marine fishes, and even perennial desert plants, population metabolism (the product of population density and energy use per individual) scales positively with body mass. This suggests that larger species use a disproportionately large share of local resources, contrary to other studies which have found population metabolism to scale either neutrally (Damuth, 1981a, 1987) or negatively (Peters, 1983) with body mass. Brown and Maurer's findings are, however, supported by those of Owen-Smith (1988), who found that population metabolism among African large herbivores increases approximately in relation to $M^{0.45}$. Thus a ten-fold increase in species body mass would be associated with an almost three-fold increase in resource use.

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Brown and Maurer suggest several advantages of large body size which may result in large species dominating

the resource allocation in ecosystems. These include: (1) dominance in interspecific aggression; (2) better predator evasion; and (3) enhanced ability to use low quality foods. However, aggressive competition for food is rare or absent among ungulate species, which instead frequently associate together, deriving mutual benefits in terms of predator avoidance (Jarman, 1974; Sinclair, 1985). Feeding by larger species may even enhance food availability for smaller species (Vesey-Fitzgerald, 1960; Bell, 1971). Further, diminished predation levels occur only among the very largest species exceeding about 1,000 kg in body mass (Owen-Smith, 1988). Enhanced tolerance for low quality foods among large herbivores (Bell, 1971; Jarman, 1974) arises from the allometry of the metabolic rate - gut capacity relationship (Demment and van Soest, 1985). Here I propose that this relationship has another important consequence for resource use in a large herbivore community. This is the ability of larger species to spread more evenly through ecosystems by feeding productively in habitats that are unsuitable for smaller species. In this section I test the hypothesis by comparing diversity of habitat use in three syntopic browsing ruminant species of widely differing body size: giraffe, kudu, and steenbok.

3.1.2 Body size and home range area

Although it is expected that large animals cover more ground than small animals, it is still unknown exactly why animals have the home ranges that they do. In a review of recent hypotheses on home range scaling, Reiss (1988) concluded that less is known about the scaling of home range area than about the dependence on size of almost any other ecological, anatomical or behavioural variable.

Home range is the area traversed by the individual in its normal activities of feeding, mating, and caring for young (Burt, 1943). This is the usual way in which home range is defined (Schoener, 1981), although a statistical alternative is to define the home range as the area within which a particular animal may be located with a specified degree of certainty (Anderson, 1982). Jewell (1966) used the term *lifetime range* to describe the total area with which an animal has become familiar, including excursions for mating and routes of movement (e.g. migrations). This term is synonymous with what Walther (1972) called the *action area*. Owen-Smith (1975), working on white rhinoceros (*Ceratotherium simum*), distinguished between the area used during all periods of the year when water was readily available (the home range), and the area used when water scarcity necessitated excursions to outlying

waterpoints (the *annual range*). In this thesis I use the home range concept as defined by Burt (*op. cit.*) to describe the area covered by adult female giraffe, kudu, impala and steenbok over the complete seasonal cycle. These species are not migratory, and as it applies to females the home range area does not include excursions for mating (as would be expected with adult males). Neither does it include excursions to water, as in this case water was always available within the home ranges of those animals dependent upon it (i.e. impala).

Early work on spatial scaling in mammals (McNab, 1963) assumed that home range area was determined by metabolic rate, which scales with body mass (M) in proportion to $M^{0.75}$ (Kleiber, 1961). This logical assumption has been invalidated, however, by subsequent analyses which have found home range area to scale with body mass exponents significantly greater than 0.75 in predatory birds (Schoener, 1968) and mammals (Harestad and Bunnell, 1979; Lindstedt *et al.*, 1986; Swihart *et al.*, 1988). Hence, increasing body size implies proportionally greater use of spatially distributed food resources than is predicted by energy requirements alone. A number of hypotheses have been advanced to explain this.

Schoener (1968) and Harestad and Bunnell (1979)

proposed that food density in the environment decreases with increasing body size, so that home range area has to *scale more steeply* than is predicted from metabolic rate. Damuth (1981*b*) suggested that home ranges of large mammals will always be larger than is predicted from individual metabolic requirements because larger species generally share their home ranges with more conspecifics. Because metabolic rate has a temporal dimension, Lindstedt *et al.* (1986) pointed out that the scaling of metabolic rate cannot be compared with the scaling of home range size without multiplying metabolic rate by some unit of time. They suggest that biological time periods (gestation, lactation or lifespan), which scale at approximately $M^{0.25}$ (reviewed by Calder, 1984), are more important than chronological time periods (days, months, years) in determining the *size of the resource base needed* by the animal. Hence home range area should scale in proportion to $M^{0.75} \times M^{0.25} = M^{1}$.

The above hypotheses, based on published estimates of home range area, assume that the area an animal covers varies as a function of the minimum area it *has* to cover in order to feed itself. In this section I investigate the validity of this assumption and the hypotheses based upon it, by analysing the relationship between home range area and body mass among four syntopic herbivore species. Marked individuals of these

species, which differ widely in body size, were concurrently monitored using the same methods, in the same area, over the complete seasonal cycle.

3.1.3 Habitat selection

In a review of 81 studies of resource partitioning among groups of organisms ranging from protozoans to large carnivores, Schoener (1974a) found that species in 90% of groups were separated by habitat. Hence separation by habitat may also be expected among African savanna ungulates, though for this group there have been few resource partitioning studies at the *habitat level*. *The two most prominent* studies were by Lamprey (1963) and Ferrar and Walker (1974), both of which included 14 ungulate species across the grazer-browser continuum. Their findings were (1) that ungulates are ecologically separated along gradients of gross vegetation structure and small scale topography (Ferrar and Walker, 1974); and (2) that this is as a result of selection for either the same habitat at different times, or different habitats at the same time (Lamprey, 1963). These findings remain unchallenged in the literature, despite the lack of statistical testing in Lamprey's study (McNaughton and Georgiadis, 1986).

It is to be expected that grazers and browsers should *have different habitat preferences as a consequence of*

their different food requirements. A more rigorous test would be to restrict the study to species from the same ungulate guild (i.e. either grazers or browsers). Here habitat preferences of four species in a browsing ruminant guild are compared during each phase of the seasonal cycle. This is to test the hypothesis that differential habitat selection is a significant factor promoting ecological separation among such species.

3.1.4 Forage [illegible] selection

Habitats [illegible] themselves resources but certain components of habitats are (Wiens, 1984). For savanna ungulates these include food, water, shade and cover. In studies on guilds it is generally assumed that resource partitioning mechanisms prevent interspecific competition for food (Schoener, 1986a). Hence it is the food component of the habitat that is relevant here, and not necessarily the habitat as a whole.

A plant community classified by ecologists in terms of species composition or physiognomy may be perceived differently by the animals feeding in it (Wiens, 1976; Senft *et al.*, 1987). This is evident from the fact that while some herbivores select habitats from a distance, most habitat selection operates by animals moving more slowly and turning more frequently in good habitats than in bad (Crawley, 1983). From the *animal-based*

perspective then, the food component of the habitat may be defined in terms of vegetation included in the foraging path.

The foraging path is governed by diet selection, which for ungulates is governed by body size, digestive system, and mouth structure (Bell, 1971; Jarman, 1974; Hofmann, 1973; Owen-Smith, 1982). It follows that differently-sized syntopic ungulate species should select distinctly different foraging paths while moving through any particular habitat feeding. Among browsers for example, the large species (e.g. giraffe) would be expected to move between palatable trees and shrubs, while the small species (e.g. steenbok) are unable to reach tree canopies, and so would be expected to move between shrubs only. Here this hypothesis is tested by comparing foraging paths selected by four species of browsing ruminant when feeding in an *Acacia* savanna.

3.2 METHODS

3.2.1 Habitat classification

A habitat for any particular species may de defined as "any part on earth where that species can live, either temporarily or permanently." (Krebs, 1985:64). In this study habitats are defined as distinct vegetation communities. Vegetation communities within the study area were identified qualitatively on the basis of dominant woody species. Mapping was done from the ground, using the central Nwamuriwa Hill as a vantage point, and was supported by aerial photography and existing large-scale landscape classifications (Gertenbach, 1983). The following habitats were classified (Fig. 3.1):

1). Hills. Granophyre hills rising distinctively above the adjacent basalt plains, represented in the study area by Nwamuriwane, Nwamuriwa, and Nkumbe hills. The latter two are the largest, rising to approximately 100 m above the surrounding landscape. The hills are well wooded with *Combretum apiculatum* and *Pterocarpus rotundifolius* being dominant species.

2). Hillbase ecotone. The base of the hills where savanna vegetation (*Acacia nigrescens* and

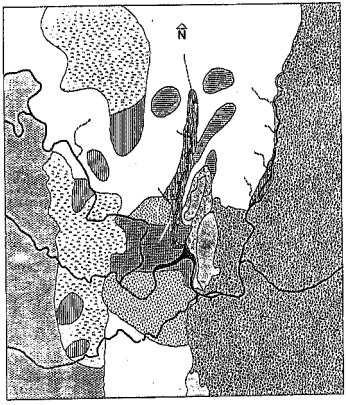

Figure 3.1. Habitats (vegetation communities) identified within the Tshokwane study area (refer to section 3.2.1). Scale: 1 cm = 1.27 km.

A. tortilis savanna, of the basalt plains meets the wooded hillslopes. The woody layer is dominated by *Combretum* and *Acacia* species, with an abundance of forbs in the herbaceous layer. In a previous study this habitat was identified by Owen-Smith (1979) as being of importance to kudu.

3). *Acacia nigrescens* savanna. The most extensive habitat, occuring on basalt plains. Characterised by knobthorn (*A. nigrescens*), marula (*Sclerocarya birrea*), and leadwood (*Combretum imberbe*) trees. The herbaceous layer is dominated by the grass *Themeda triandra*.

4). *Acacia tortilis* savanna. Also occurs on basalt plains, but tends to be restricted to the vicinity of pans and riverlines. The woody layer is dominated by umbrella thorn (*A. tortilis*) and the grass cover is typically overgrazed, mainly by impala and wildebeest. Forbs are abundant in the wet season. Represented in the study area in the region of Tshokwane ranger station, on either side of the Nwaswitsontso River.

5). *Acacia tortilis / A. nigrescens* ecotone. An intermediate habitat at the interface of the above two. *A. nigrescens* and *A. tortilis* trees are both well represented, with more grass cover (mainly

Themeda triandra) than in the *A. tortilis* savanna.

6). *Acacia gerrardii* savanna. Small patches within the *A. nigrescens* savanna that are dominated by red thorn (*A. gerrardii*). Situated in areas of poor drainage.

7). *Acacia welwitschii* thicket. Dense monospecific stand of Delagoa thorn (*A. welwitschii*) growing on Karoo sediments, which separate the granitic and basaltic soil types of the central KNP. Occurs on the western edge of the study area.

8). Mixed woodland. An association of woody vegetation characterised by the presence of *Terminalia sericea* (although not always common), and also *Dichrostachys cinerea*, *Albizia harveyii*, and *Peltophorum africanum*. This habitat includes Kumana sandveld (Gertenbach, 1983) on an exposed Karoo sediment anticline (Coetzee, 1983) in the north-western part of the study area.

9). *Albizia petersiana* thicket. Monospecific stands of *A. petersiana* growing in low-lying areas in pockets of Karoo sediments, closely associated with the above habitat type.

10). Lebombo Range. Low rhyolite hills, forming part of

the chain of Lebombo Mountains that mark the eastern boundary of the KNP with Mocambique. The woody vegetation is dominated by scrubby stands of *Combretum apiculatum* and *C. hereroense*. *Acacia nigrescens* and *Peltophorum africanum* are common. The soils are generally thin and rocky.

11). *Dichrostachys cinerea* scrub. Sickle bush (*D. cinerea* subsp. *africana*) in dense stands in places, associated with *A. tortilis*, *Grewia* spp, and *Euclea divinorum* within the loops of the Nwaswitsontso River. Many of the *D. cinerea* plants are senescent and dying back.

12). *Lonchocarpus* belt. Region of the lower catenary sequence within *Acacia nigrescens* savanna in which apple-leaf (*L. capassa*) is common. Occurs along either side of the Nkongwana Watercourse and Hetsi Hetsi River.

13). Watercourse. Drainage lines within *Acacia nigrescens* savanna characterised by the presence of fever trees (*A. xanthophloea*), but lacking a riverbed and large broad-leaved trees.

14). Riverine. Thick woody vegetation growing on the banks of rivers such as the Nwaswitsontso and its tributary, the Hetsi Hetsi. Characterised by large

broadleaved trees such as *Ficus sycamorus*, *Diospyros mespiliformis*, *Schotia brachypetalia*, and *Kigelia africana*. The wild date palm (*Phoenix reclinata*) overhangs the banks, with reeds (*Phragmites mauritianus*) growing in the sandy riverbed.

3.2.2 Animal distributions

The distribution of study animals among habitats was monitored through the seasonal cycle by use of radio telemetry, and in the case of steenbok by counting animals flushed from random transects through the study area.

During the course of the study, radio transmitters were placed on two steenbok, two impala, four kudu, and three giraffe. A further three marker collars (without transmitters) were placed on impala. With the exception of one giraffe, all collared animals were females. Females were chosen to avoid the possibility of damage to transmitters and strangulation of males during fighting. Mortality (presumably by predation) prevented the use of data from some animals (Table 3.1).

Collars were attached to animals located as close as possible to Nwamuriwa Hill, in the centre of the study area. This was to ensure that data were collected from

Table 3.1. Information on study animals marked with radio collars or neck bands.

Species	ID code	Period monitored (months)	Location points per season			Mortality	Data used
			Wet	Dry	Total		
Giraffe	G915[a]	1	7	8	15	X	
"	G921	0.75	0	9	9	X	
"	G920	27	93	89	182		X
Kudu	K900	32	84	112	196		X
"	K905	23	27	74	101	X	X
"	K910	31.75	52	77	129		X
"	K915	31	25	48	83		X
Impala	I909	12	40	38	78		X
"	I912	12.75	32	21	53		X
"	I91[b]	12.75	15	8	23		X
"	I92[b]	6	9	6	15	X	
"	I93[b]	12	19	13	32		X
Steenbok	S905	10	15	13	28	X	X
"	S907	10.25	22	24	46	X	X

[a]Male, all others female.
[b]Marked with neck bands, all others with radio collars.

coexisting populations. The hill also provided an ideal vantage point for commencing daily tracking. Collars were attached to selected animals after immobilisation with M99 (Etorphine hydrochloride) injected by dart from a vehicle. Transmitters (Telonics and AVM) built into collars made of machine belting were placed around the neck in all cases. Collars did not appear to influence behaviour, and all collared giraffe, kudu, and impala females gave birth subsequently to healthy young. All collars were removed at the end of the study.

Radio tracking was conducted from a 4-wheel-drive vehicle mounted with a directional "Yagi" antenna on a collapsible 2 m mast. The mast could be rotated through 360° from inside the vehicle or locked in position for reading bearings off a compass card at its base. The bearing corresponding to the best signal strength received, when added to the magnetic orientation of the vehicle, provided a magnetic bearing to the collared animal. By triangulation a quick estimate of the general map positions of collared animals could be made. The selected animal would then be homed in on by driving with the antenna locked in the straight ahead position and steering the vehicle so as to maintain the best signal strength received through headphones.

Radio tracking was usually done in the early morning,

and once located the focal animal was normally used for feeding behaviour studies for the rest of the day. A different animal would be selected on the following day. Each location was plotted as the position at which contact was first made, and so consecutive locations were always separated by a period of at least 24 hours. The time interval was sufficient to allow "time-to-independence" between successive locations, as calculated for giraffe (the largest species) by the formula of Swihart *et al.* (1988). This prevented autocorrelation of location data (see also Schoener, 1981).

Map coordinates (using a 1:50,000 map for steenbok, impala, and kudu; and a 1:100,000 map for giraffe) were recorded, together with details of size and composition of the group associated with the collared animal, habitat type, and date. Every effort was made to spread observations evenly over the seasonal cycle (Table 3.1).

3.2.3 Habitat use

1. Kudu

The four kudu cows that were collared were chosen from separate but adjacently situated social units (groups of adult and subadult cows, calves, and yearling males,

referred to henceforth as "cow groups"). Only one other cow group occurred within the distribution of these four. This meant that the distribution of most of the *kudu population* in the study area could be effectively monitored over a range of habitats by radio tracking one cow *in each of the four separate groups*. Habitat use by each cow group was quantified for each quarter of the seasonal cycle (refer to *Fig. 3.2*) by radio tracking the collared cow, counting the animals associated with her, and recording the habitat they were found in. The subtotal of animals counted in each habitat was then calculated for each quarter for each cow group. The number of times that each group was located by radio tracking was also totalled for each quarter and then averaged across groups to derive an average radio tracking effort (n_a) for each quarter. A weighting (w) was calculated as

$$w = n_a / n_i$$

where n_i is the number of times that the ith kudu group was actually tracked down. The quarterly subtotal of animals from the ith group found in each habitat was then multiplied by w, equalising tracking effort across the four groups. Weighted data for the four groups were then combined for each quarter, and proportions of the weighted total kudu count were calculated for each habitat. This method was employed to measure the

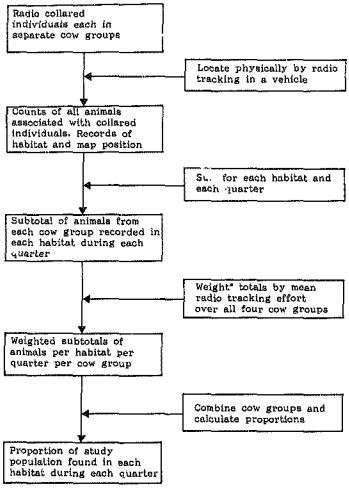

Figure 3.2. Process by which proportional habitat use was calculated for kudu during each quarter of the seasonal cycle (January-March, April-June, July-September, October-December).
*Weighted by w (see section 3.2.3).

distribution of the complete study population of kudu (not just the cow groups) among habitats. Where independence of sampling was required for statistical reasons, the cow group (irrespective of size) was used as the unit of measurement (section 3.2.7).

ii. Giraffe

Unlike kudu, giraffe do not occur in stable social units but are gregarious, in that they drift from group to group over a wide area (Foster and Dagg, 1972; personal observations). Hence by systematically locating one radio collared cow as she moved over a large home range (which encompassed the entire study area), a loose aggregation of giraffe would be located on each occasion. The number of animals in the aggregation was recorded each time, together with the habitat they were located in. Subtotals of animals located in this way in each habitat were calculated for each quarter of the seasonal cycle. Subtotals were converted to proportions by dividing by the quarterly grand total of animals counted over all habitats.

iii. Impala

Impala are highly gregarious, occurring in large "clans" (Murray, 1982) which may number up to 300 individuals in the central KNP (personal records).

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iii. Impala

Impala are highly gregarious, occurring in large "clans" (Murray, 1982) which may number up to 300 individuals in the central KNP (personal records).

Consequently it was extremely difficult to count the animals associated with each collared individual. This problem, coupled with the fact that each clan moves over a small range of habitats made it impossible to obtain reliable habitat use data for impala over the whole study area. Consequently radio telemetry data were used only to estimate individual home range sizes (to be described later) and monitor cross-catenary movements between seasons (Chapter 4).

iv. Steenbok

Steenbok are solitary and remain within small ranges, so radio telemetry using two animals was inadequate for monitoring habitat use. Being cryptic by habit, steenbok are difficult to locate by eye. However, the anti-predator behaviour of steenbok is to remain hidden as long as possible and then burst from cover, running in a zig-zag fashion for approximately 100 m, and then freezing. This made it possible to count steenbok flushed by the vehicle when driving slowly on random transects through the study area. Differences between habitats in terms of visibility could cause some unavoidable bias in this method. This is minimized, however, by the fact that although steenbok are extremely cryptic when lying down, they are very obvious when dashing from cover at close quarters, regardless of habitat density. As with

giraffe, the subtotal of sightings recorded in each habitat during each quarter was divided by the quarterly grand total to give the proportion of steenbok sightings in each habitat during each quarter.

Over the entire study period the total number of records per study species was 4,508 for kudu, 883 for giraffe, and 349 for steenbok (one record = one animal marked present in a habitat).

3.2.4 Habitat availability

Habitat "availability" to a study population was measured as the proportional area of each habitat occurring within the total area available to that population. Areas were measured using a dot planimeter.

For kudu, the total area available was determined by including each grid square (1 km^2) on a 1:50,000 map in which a collared animal had been sighted. This method ensured that all habitats falling within (at most) 1 km of sites known to have been used by study animals were included as being available. If home range boundaries had been used, habitats bordering on the home range would have been erroneously excluded from those considered to be available. The choice of a 1 km^2 grid was arbitrary and convenient, but of a realistic scale since a distance of 1 km would be easily covered by a

kudu during a foraging spell (personal records).

Steenbok sightings were made at random on unmarked animals while traversing the study area, and the portion of the study area traversed most frequently was that used by the study population of kudu. Hence this area was chosen to represent that available to the sample of the steenbok population used here to assess habitat use. Only those steenbok sightings recorded within this area were used, and so the areas of habitats considered available are the same as those for the kudu population.

Giraffe habitat use was determined from the giraffe found to be associated with a collared female (G920, see Table 3.1). The habitats considered available in this case were those within the area determined by including each grid square (4.89 km^2) on a 1:100,000 map in which the collared female was sighted. The rationale for using this method is the same as that described for kudu. The difference in spatial scales used for kudu and giraffe is approximately proportional to the difference in body mass between the two species.

3.2.5 Diversity of habitat use

Diversity of habitat use was estimated for giraffe, *kudu, and steenbok. For each species during each*

quarter, proportional use of each of the 14 habitats in the study area was calculated as:

$$p_{ij} = \frac{n_{ij}/p_{ai}}{\Sigma(n_{ij}/p_{ai})}$$

where p_{ij} is the proportion of the study population using the ith habitat during the jth quarter when all habitats are equalized by area; n_{ij} is the subtotal of study animal sightings in the ith habitat for the jth quarter (section 3.2.3); and p_{ai} is the proportional availability by area of the ith habitat (section 3.2.4). For each species the values of p_{ij} were averaged across quarters to give P_i, the proportion of study animals using the ith habitat of equalized area, on average, throughout the year. The Shannon-Wiener index H' (Shannon and Weaver, 1949) was used to indicate diversity of habitat use, calculated as

$$H' = -\Sigma\ P_i \log P_i .$$

The use of H' as an index of ecological diversity has been criticised by some (e.g. Hurlbert, 1971), who consider information theory (upon which the index is based) unsuitable for ecological applications. As pointed out by Pielou (1977) and Brower and Zar (1977) though, the index should be viewed as an index of "uncertainty". In the present case, if an individual of

a particular browser species was picked at random, there would be much uncertainty in predicting which *habitat* it was removed from if the diversity of habitats used by that species was high. In this context *H'* has properties that make it particularly suited to ecological applications (Pielou, 1977).

3.2.6 Home range

3.2.6.1 *Estimation of home range area*

All locational data collected by either radio telemetry or direct observation were plotted on a separate map overlay for each collared animal. Each location point was the position at which that animal was first sighted on a particular day. In each case the outermost points of the complete sample were connected in the minimum convex polygon (MCP) method of home range area estimation (Southwood, 1978; White and Garrott, ms.). *MCP areas (in km²) were measured with a dot planimeter.*

A major criticism of the MCP method is that it has a sample size bias in that the area estimate tends to increase as the number of location points (*n*) increases. It is nevertheless defended by Jennrich and Turner (1968) because of its simplicity, and though these authors provide a means of correcting for bias, this is only applicable when samples are small

($n < 25$). Schoener (1981), in an extremely thorough test of home range area estimation techniques, also defended the MCP method as being simple and appropriate for animals whose home ranges are truly convex, as should be expected in fairly uniform habitats. He found that although MCP estimates are strongly affected by sample size, the effect virtually disappears at $n = 25$. Furthermore, the larger the time interval between successive observations, the less important the sample size effect. Hence the use of the MCP method in this study is justified by the generally large sample sizes, made up of statistically independent observations, collected over long periods (Table 3.1). As Jennrich and Turner (1969) pointed out, any home range area estimation is strictly an *index* of home range area, and in this study it is the relationship between indices that is being considered.

Alternative methods to the MCP are numerous and elaborate (reviewed by Anderson, 1982; White and Garrott, ms.), requiring computer facilities. This drawback reduces their advantages over the MCP method, particularly when analyses are being performed under field conditions. It is possible to improve on the MCP estimate by eliminating outlying points resulting from rare wanderings, and including 95% of location points. Deciding on which points to eliminate is problematic

though, and also requires complex software (White and Garrott, ms.).

3.2.6.2 *The scaling of home range area with body mass*

The relationship between home range area and body mass was determined by linear regression analysis, using the SAS REG procedure (SAS Institute Inc., 1985*b*). This *method* assumes that values on the *x* axis are measured without error (Harvey and Mace, 1982), but this assumption is usually impossible to satisfy and considering the range in body mass values used, slight errors for each species are negligible (Zar, 1984).

MCP areas were averaged for each species (excluding giraffe, for which only one estimate could be *derived*). Mean estimates per species were used to avoid bias in the regression analysis (see Harvey and Mace, 1982). This bias is caused when a cluster of data-points (e.g. individual MCP areas) significantly influences a relationship but in fact represents only one point (e.g. the home range area estimate for a species). Body mass estimates were assigned to study animals on the basis of published body mass values for adult females (Smithers, 1983; Owen-Smith, 1988) as follows: giraffe, *800 kg*; kudu, *180 kg*; *impala*, *41 kg*; *steenbok*, *11 kg*. Note that the giraffe estimate is ± 20 kg lower than the published mean, as the collared animal was fairly

young and slight in comparison with other mature cows. The kudu estimate is ± 10 kg higher than the published mean because large cows were intentionally selected for collaring. It was hoped that these would be the oldest and most habituated to vehicles from previous studies in the area.

3.2.7 Habitat preference

i. Goodness of fit

A chi-square goodness of fit test was performed to test for significant differences between "expected" use of habitats (based on proportional habitat availability by area) and observed frequency of usage by giraffe, kudu, and steenbok during each quarter of the seasonal cycle. The objective was to determine if these species are in fact selective at the habitat level. The chi-square test is used under the assumption that observations are independent, which precludes the analysis of aggregated animals (Alldredge and Ratti, 1986). Hence, because giraffe and kudu occur in aggregations, the frequency of radio tracking locations made in each habitat was used to indicate habitat use rather than the number of animals counted (i.e. one group = one observation). As with home range estimation, only one observation was used per marked animal per day, allowing time-to-independence between successive observations and so

preventing autocorrelation of locational data (Swihart *et al.*, 1988). In the case of steenbok, for which habitat use was estimated from counts of animals flushed from random transects, each sighting represented one observation regardless of whether the sighting was of a pair or an individual. The *chi-square* test was applied under the conditions of Roscoe and Byars (1971), that the average (over all categories) expected observation is six or more for a significance level of at least 0.01. To meet this requirement, some categories (habitats) had to be combined.

To test for seasonal differences in habitat use, the chi-square test of homogeneity (Brown and Hollander, 1977) was performed for each species. This was done by pooling observed frequencies of habitat use for the four quarters of the year in a 4 x *k* contingency table (*k* being the number of habitat categories). The null hypothesis was that patterns of habitat use do not change through the seasonal cycle.

ii. Preferences for specific habitats

To identify habitats that contribute most to the chi-square statistic for each goodness of fit test, simultaneous confidence intervals were constructed for proportions of observations recorded in each habitat, using the Bonferroni method (Neu *et al.*, 1974; Byers *et*

al., 1984). By this method 95% confidence intervals around observed proportions of usage (p_{oi}) in all habitats are calculated as

$$p_{oi} \pm z_{(1-\alpha/2k)}\sqrt{[p_{oi}(1-p_{oi})/N]},$$

where $z_{(1-\alpha/2k)}$ is the normal table value corresponding to a probability area of $1-\alpha/2k$ (in this case $\alpha = 0.05$); k is the number of habitats in the test; and N is the total number of observations over all habitats. If the expected proportion of observations for a particular habitat lies outside of the 95% confidence interval about the observed proportion, then use of the habitat may be considered significantly different to that "expected".

Use of the above method assumes the sample size is sufficiently large for a normal distribution approximation to the binomial distribution to be valid. Hence confidence intervals were constructed only for p_{oi} when $N(1-p_{oi})$ and Np_{oi} were both ≥ 5 (Alldredge and Ratti, 1988).

Although impala habitat preferences could not be determined over the complete study area, locational data for collared individuals were used to monitor seasonal movements across the catenary drainage sequence. Of the total monthly sightings of collared

individuals, the percentage of those that were made in riverine vegetation was calculated for each month. This percentage was then compared with rainfall statistics for each month using simple linear correlation analysis. Four rainfall statistics were used: monthly rainfall (in mm); the 2-month running mean of rainfall (2-MRMR), calculated (also in mm) as rainfall averaged over the month in question and the preceding month; 3-MRMR, averaged over the month in question and the preceding 2 months; and 4-MRMR, averaged over the month in question and the preceding 3 months (see also Chapter 4, section 4.2.6).

iii. Habitat preference comparisons

To compare habitat preferences among species, a habitat *preference index* (*HPI*) was derived for each of the habitats used by giraffe, kudu, and steenbok during each quarter of the seasonal cycle. Proportional habitat use (p_{ui}) was divided by proportional habitat availability (p_{ai}) within the areas used by each of the study populations:

$$HPI = p_{ui}/p_{ai}.$$

In this case p_{ui} was the proportion of all animals counted in the ith habitat as determined by the method described in section 3.2.3. This type of preference

index (Ivlev, 1961) varies asymmetrically from zero towards infinity as habitat use increases in proportion to availability. A value >1 means that use is proportionally greater than availability, which by convention indicates preference while a value <1 indicates avoidance (Crawley, *1983*). The index has its limitations (Alldredge and Ratti, 1986; Owen-Smith and Cooper, 1987a) but is useful for sorting habitats along a preference axis. Using log-transformed *HPI* values (to rectify the asymmetry problem), habitat preferences were compared among species for each quarter of the year using simple correlation analysis. The SAS CORR procedure was used (SAS Institute Inc., 1985a).

3.2.8 Foraging path comparisons

The foraging path of a large herbivore is defined here as *vegetation immediately available to that herbivore while foraging through a particular habitat*. Such vegetation occurs in the foraging path by virtue of selection for certain food plants, and the association of other plants with these food plants. Vegetation "immediately available" consists of plants bearing edible parts within a distance of the animal such that they may be selected immediately after the termination of feeding on the previous plant. Measuring this distance is difficult, but the shorter the distance, the greater the probability of an included plant being

within selection distance. The shorter the distance, however, the smaller the sample of plants classified as available. An arbitrary distance of 5 m was chosen since it is easily estimated in the field, includes an adequate sample of plants (for statistical purposes), and was not found to be unrealistically large for the smallest study animal, the steenbok.

While recording habitat-specific feeding observations on a focal animal, all woody plant species within a radius of 5 m of its mouth were noted during every fifth woody plant feeding event (see Chapter 4). This method generated lists of woody plant species occurring in the foraging paths of each browser species, and for each plant species a measure of the frequency of its occurrence in each foraging path. Only woody plant species were recorded, as forbs and grasses were impossible to identify quickly and accurately through binoculars from a vehicle. Woody plants recorded were those with foliage in the feeding height range of the focal animal. Availability was recorded at every fifth woody plant feeding station to ensure independence of sampling, as all study animals moved more than 5 m (the radius of the sampling area) during the course of five successive woody plant feeding events. An alternative method, which has been used with tame kudu, is to record species present within 10 m of the focal animal during successive 30 minute periods (Owen-Smith and

Cooper, 1987a). This method is impractical when observing wild animals from a vehicle, however, and in this case regular "snapshot" sampling over a smaller area is more applicable. Furthermore, selection only takes place when an animal actually chooses a food item from others available (Johnson, 1980), and so availability measurements are most relevant when recorded in the immediate vicinity of the *feeding site* at the time of feeding.

The habitat most suitable for testing differences *between foraging* paths was *Acacia tortilis* savanna. This habitat was commonly used by giraffe, kudu, impala, and steenbok during wet and dry seasons. An additional comparison was made between the foraging paths of giraffe and kudu in *A. nigrescens* savanna. For each browser in the habitat concerned, all availability records made along the foraging path were combined for the complete seasonal cycle. The chi-square test of homogeneity usually used to test the validity of combining data-sets (Brown and Hollander, 1977) is inapplicable in this case, since abundance of foliage on woody plants varies naturally between wet and dry seasons. However, it is assumed that seasonality had the same effect on woody browse availability for all species as foraging path comparisons were restricted to a habitat used by all study populations throughout the year.

Pair-wise comparisons of foraging paths were performed in each case using the chi-square test on a 2 x *k* contingency table. A chi-square value was calculated for each of the *k* plant species (or groups of plant species when *expected frequencies* were <5) in each foragirg path pair. The sum of these chi-square values constitutes the chi-square statistic for the overall analysis. If the test found a significant difference between foraging paths, then for plants contributing a chi-square value >2 to the overall chi-square statistic, the proportions of occurrence of these plants were calculated in both foraging paths. For each such plant, a 95% confidence interval was constructed about its observed proportion of occurrence in the foraging path in which it was more common. The Bonferroni method was used as described in section 3.2.7 (Neu *et al.*, 1974; Byers *et al.*, 1984). By comparing in each case the confidence interval with the *proportion of occurrence* of the same plant in the other foraging path, plants that distinguished one foraging path from the other were statistically isolated in each pairwise comparison.

3.3 RESULTS

3.3.1 Body size and habitat specialisation

Values of the Shannon-Wiener index (H'), calculated to indicate diversity of habitat use, are: steenbok, 0.78; kudu, 0.85; giraffe, 0.93. A double logarithmic plot of H' against body mass (Fig. 3.3) shows that although all three species occurred throughout the study area, steenbok specialised on a narrower range of habitats than kudu, which in turn were less evenly distributed than giraffe

3.3.2 Body size and home range area

Estimates of mean home range area per study species (Table 3.2, and see Appendix A), calculated from MCP areas for collared individuals, are: steenbok, 0.62 km^2; impala, 5.81 km^2; kudu, 21.9 km^2; and giraffe, 282 km^2. The relationship between home range area and body mass (Fig. 3.4) is described by the following equation:

$$Ahr = 0.024\ M^{1.38},$$

where Ahr is home range area in km^2, and M is body mass in kg ($r^2 = 0.99$, $P < 0.01$). The 95% confidence interval about the body mass exponent is 1.01 - 1.75.

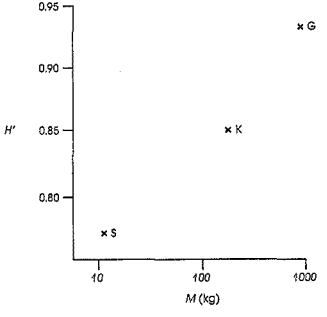


Figure 3.3. Diversity of habitat use (H') plotted against body mass (M) for steenbok (S), kudu (K), and giraffe (G). Axes are logarithmic.

Table 3.2. Home range area estimates.

Species	ID code*	Area (km^2)
Giraffe	G920	282
Kudu	K900	7.87
"	K905	32.4
"	K910	22.8
"	K925	24.4
"	Mean	21.9
Impala	I909	5.30
"	I912	6.94
"	I91	5.31
"	I93	5.70
"	Mean	5.81
Steenbok	S902	0.52
"	S907	0.73
"	Mean	0.62

*See Table 3.1 and Appendix A for sample sizes.

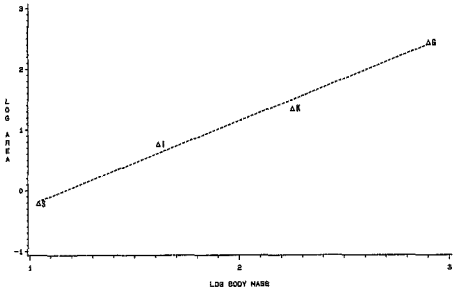


Figure 3.4. Double-logarithmic plot of the relationship between home range area (km^2) and body mass (kg). Points represent mean home range area estimates for steenbok (S), impala (I), kudu (K) and giraffe (G). Refer to Table 3.2 for areas covered by individuals of each species.

3.3.3 Habitat preference

1. Goodness of fit

Chi-square statistics (Table 3.3) show that habitat use by kudu and steenbok deviated significantly from expected on the basis of habitat availability, during each quarter of the year. This indicates that these species select certain habitats in preference to others throughout the seasonal cycle. In the case of giraffe, habitat use deviated from expected only during the 3rd and 4 h quarters of the year (late dry season and early wet season).

Chi-square tests of homogeneity found that habitat use by giraffe and kudu differed significantly between *seasons* (giraffe $chi^2_{calc} = 53.88$, $chi^2_{0.001,9} = 27.88$; kudu $chi^2_{calc} = 64.18$, $chi^2_{0.001,24} = 51.18$). In the case of steenbok, though, habitat use remained unchanged throughout the seasonal cycle ($chi^2_{calc} = 11.77$, $chi^2_{0.05,9} = 16.92$).

ii. Preferences for specific habitats

Considering each habitat independently for giraffe (Table 3.4), weak selection was detected for the Lebombo Range in the late wet season, and watercourses and riverlines were strongly preferred in the late dry

Table 3.3. Chi-square statistics for habitat goodness of fit tests.

Quarter[a]	Calculated chi-square statistics[b]		
	Giraffe	Kudu	Steenbok
1	7.13	50.12*	250.15*
2	6.75	101.62*	242.09*
3	364.37*	352.40*	176.37*
4	53.43*	100.76*	496.83*

[a]1, January-March; 2, April-June; 3, July-September; 4, October-December.
[b]Values of K: giraffe, 4; kudu, 13; steenbok, 6.
*$P < 0.05$.

Table 3.4. Giraffe habitat preferences.

Habitat	Expected proportion (p_{oi})[a]	Observed proportions (p_{oi})[a] of giraffe locations per habitat per quarter[b], with 95% intervals[c]											
		1st quarter (N = 45)			2nd quarter (N = 25)			3rd quarter (N = 47)			4th quarter (N = 42)		
		p_{oi}	95% Interval	Pref[d]	p_{oi}	95% Interval	Pref	p_{oi}	95% Interval	Pref	p_{oi}	95% Interval	Pref
Hills	0.021	0			0			0			0.024		
Hillcrest acetose	0.015	0.022			0			0.064			0.143	0.000-0.295	0
Acacia nilpescens savanna	0.152	0.067			0.120			0.340	0.141-0.530	0	0.286	0.085-0.487	0
Acacia tortilis savanna	0.048	0.222	0.044-0.400	0	0.040			0			0.095		
Acacia tortilis/ *A. nilpescens* acetose	0.007	0			0.040			0.064			0.024		
Acacia gerrardii savanna	0.015	0			0.080			0			0		
Acacia welwitschii thicket	0.048	0			0.040			0			0.024		
Mixed woodland	0.198	0.133	0.006-0.279	0	0.080			0.064			0		
Albizia petersiana thicket	0.060	0			0.040			0			0		
Lebombo Range	0.197	0.444	0.227-0.667	+	0.360	0.021-0.539	0	0.042			0.190	0.014-0.364	0
Dichrostachys cinerea scrub	0.012	0			0.200			0			0		
Combocarpus belt	0.017	0.067			0			0			0.071		
Watercourses and riverlines	0.022	0.044			0.080			0.426	0.277-0.533	+	0.143	0.000-0.298	0

[a]Calculated for the ith habitat as $p_{oi} = n_i/N$, where n_i is the number of times giraffe were located in that habitat.
[b]Quarters of the year: 1/4, January-March; 2/4, April-June; 3/4, July-September; 4/4, October-December.
[c]Confidence intervals calculated only for p_{oi} when $p_{oi}(N) \geq 5$.
[d]Proportion expected if habitat use was proportional to habitat availability by area.
[e]*Preference*: +, use significantly greater than expected; -, use significantly lower than expected; 0, use no different to expected.

Table 3.5. Kudu habitat preferences.

Habitat	Expected proportion (a_w)[a]	Observed proportions (p_{wr})[a] of kudu locations per habitat per quarter[b], with 95% intervals[c]											
		1st quarter (N = 125)			2nd quarter (N = 64)			3rd quarter (N = 224)			4th quarter (N = 169)		
		p_{wr}	95% interval	Pref[d]	p_{wr}	95% interval	Pref	p_{wr}	95% interval	Pref	p_{wr}	95% interval	Pref
Hills	0.045	0.125	0.053–0.237	0	0.203	0.069–0.347	+	0.147	0.079–0.215	+	0.046	0.000–0.104	0
Hillbush	0.044	0.133	0.032–0.258	0	0.203	0.069–0.347	+	0.228	0.147–0.308	+	0.183	0.084–0.281	+
Acacia nigrescens savanna	0.554	0.486	0.317–0.655	0	0.266	0.167–0.424	-	0.307	0.246–0.449	-	0.533	0.395–0.669	0
Acacia tortilis savanna	0.041	0.014			0.125	0.000–0.244	0	0.067	0.019–0.115	0	0.018		
Acacia tortilis/ A. nigrescens ecotone	0.022	0.008			0.062			0.016			0		
Acacia gerrardii savanna	0.047	0			0.047			0.009			0.027		
Mixed woodland	0.045	0.069	0.000–0.155	0	0			0			0		
Albizia petersiana thicket	0.011	0			0			0			0		
Lebombo range	0.065	0			0			0.009			0.018		
Dichrostachys cinerea scrub	0.030	0			0			0			0		
Combretum belt	0.065	0.120	0.032–0.256	0	0.062			0.058	0.015–0.103	0	0.064	0.000–0.131	0
Watercourses and riverlines	0.027	0			0.031			0.107	0.048–0.166	+	0.101	0.018–0.184	0

[a]Calculated for the ith habitat as $p_{wi} = n_i/N$, where n_i is the number of times kudu were located in that habitat.
[b]Quarters of the year: 1/4, January–March; 2/4, April–June; 3/4, July–September; 4/4, October–December.
[c]Confidence intervals calculated only for p_{wi} when $p_{wi}(1-p_{wi}) \geq .5$.
[d]Proportion expected if habitat use was proportional to habitat availability by area.
[e]Preference: +, use significantly greater than expected; -, use significantly lower than expected; 0, use no different to expected.

Table 3.6. Steenbok habitat preferences.

Habitat	Expected proportion (p_{oi})[a]	Observed proportions (p_{oi})[a] of steenbok sightings per habitat per quarter[b], with 95% intervals[c]											
		1st quarter (N = 69)			2nd quarter (N = 44)			3rd quarter (N = 59)			4th quarter (N = 161)		
	p_{oi}	95% interval	Pref[d]	p_{oi}	95% interval	Pref	p_{oi}	95% interval	Pref	p_{oi}	95% interval	Pref
Hills	0.045	0		0			0			0		
Hillbase	0.044	0.034		0.045			0			0.112	0.041–0.183	0
Acacia nilotica savanna	0.564	0.086	0.049–0.182	-	0.091		0.248	0.161–0.413	-	0.217	0.124–0.310	-
Acacia tortilis savanna	0.361	0.517	0.330–0.705	+	0.545	0.329–0.760	+	0.490	0.277–0.593	+	0.453	0.348–0.565	+
Acacia tortilis/ A. nilotica acotone	0.022	0.121	0.069–0.144	0	0.182			0.100	0.000–0.222	0	0.031	0.016–0.143	0
Acacia garrardii savanna	0.047	0.017			0.045			0.020			0		
Mixed woodland	0.045	0			0			0.020			0		
Albizia petersiana thicket	0.011	0.017			0			0			0		
Lebombo range	0.000	0.017			0			0.020			0.006		
Combretum/Acacia nilotica scrub	0.020	0.086	0.000–0.192	0	0.068			0			0.006		
Enneapogon cenchroides belt	0.065	0.103	0.000–0.217	0	0.023			0.040			0.037	0.000–0.080	0
Watercourses and riverlines	0.027	0			0			0.000			0.007	0.000–0.051	0

[a]Calculated for the ith habitat as $p_{oi} = a_i/A$, where a_i is the number of times steenbok were sighted in that habitat.
[b]Quarters of the year: 1/4, January–March; 2/4, April–June; 3/4, July–September; 4/4, October–December.
[c]Bonferroni intervals calculated only for p_{oi} when $p_{oi}(A) \geq 5$.
[d]Proportion expected if habitat $_i$ was proportional to habitat availability by area.
[e]Preference: +, was significantly greater than expected; -, was significantly lower than expected; 0, was no different to expected.

season. Kudu (Table 3.5) also selected riverlines and watercourses in the late dry season, as well as the hills throughout the dry season, and the hillbase ecotone through the dry season and early wet season. *Acacia nigrescens* savanna was used significantly less than expected from availability in the dry season. Steenbok (Table 3.6) exhibited a particularly strong preference for *Acacia tortilis* savanna throughout the year, while *A. nigrescens* savanna was generally used significantly less than expected from availability.

With impala there was a very clear seasonal shift in habitat use, from savanna habitats of the upper catena in the wet season to the riverine habitat in the dry season. The monthly percentage of collared impala sighted in the riverine habitat was strongly negatively related to the 3-MRMR (r = -0.85, P = 0.0005; Fig. 3.5).

iii. Habitat preference comparisons

HPI values (Table 3.7) reflect the habitat preferences detected by the Bonferroni method. In the case of giraffe, particularly high preferences were detected for *Dichrostachys cinerea* scrub in the 2nd quarter of the year when *D. cinerea* are in pod. The riverine habitat also scored a high preference rating in the 3rd quarter (late dry season), as did the *Acacia*

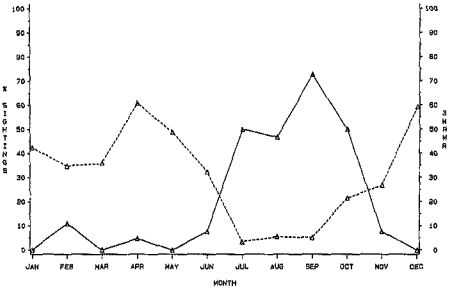


Figure 3.6. Sightings of collared impala in riverine habitat (solid line) during each month from January to December 1986 (as a percentage of the total sightings over all habitats for each month in question), plotted with the 3-month running mean of rainfall (3-MRMR) in mm (dashed line).

Table 3.7. Habitat preference index (HPI) values.

Habitat	HPI values during each quarter[1] of the seasonal cycle											
	Giraffe				Kudu				Steenbok			
	1/4	2/4	3/4	4/4	1/4	2/4	3/4	4/4	1/4	2/4	3/4	4/4
Hills	-	-	-	0.79	3.13	5.66	4.46	1.23	-	-	-	-
Riffhaas	1.15	-	5.67	5.42	3.36	4.89	6.67	6.82	0.70	0.92	-	2.51
Acacia nigrescens savanna	0.16	0.40	0.82	0.77	0.86	0.42	0.48	0.68	0.16	0.18	0.40	0.36
Acacia tortilis savanna	5.13	0.59	-	1.42	0.40	2.22	1.64	3.65	0.48	0.73	0.37	1.99
Acacia tortilis/A. nigrescens acotone	-	2.39	12.81	3.43	0.71	3.46	0.38	-	4.90	0.24	5.93	3.51
Acacia perrarotii savanna	-	2.50	-	-	-	0.24	5.99	3.68	0.67	0.67	0.37	-
Acacia welwitschii thicket	-	0.85	-	0.55	-	-	-	-	-	-	-	-
Mixed woodland	0.63	0.44	0.32	-	1.22	-	-	-	-	-	0.39	-
Albizia petersiana thicket	-	0.81	-	-	-	-	-	-	1.43	-	-	-
Lebombo Range	2.10	1.27	0.30	1.32	-	-	0.07	0.35	0.26	-	0.29	0.00
Dichrostachys cinerea scrub	-	16.35	-	-	-	-	-	-	3.94	4.16	-	0.28
Ironbarkcorpus bolt	5.40	-	-	3.94	1.96	0.48	0.89	1.34	2.69	0.37	0.64	0.44
Watercourse	9.33	-	6.08	6.79	-	5.90	4.72	4.65	-	-	4.84	5.11
Riverine	-	6.11	26.26	7.76	-	-	2.48	3.94	-	-	1.55	0.42
Sample size[2]	199	148	101	235	447	591	2468	1023	64	49	97	179

[1]1/4, January-March; 2/4, April-June; 3/4, July-September; 4/4, October-December.
[2]Total number of records per q year (one record = one animal marked present in a habitat).

tortilis/A. nigrescens ecotone. A high preference for the latter habitat, which in the study area occurs near the Nwaswitsontso River, is probably a consequence of attraction to green foliage in the riverlines on the one hand, and flowering *A. nigrescens* on the other. For kudu, the hills and hillbase habitats scored consistently high preference ratings, and the watercourse and riverine habitats rated highly in the 2nd - 4th quarters (dry and early wet seasons). Steenbok *HPI* values clearly reflected the consistently strong preference for *Acacia tortilis* savanna and its ecotone with *A. nigrescens* savanna. Some preference was also detected for the watercourse habitat in the 3rd and 4th quarters.

Comparing *HPI* values across species for each quarter by *simple correlation analysis, only one significant* relationship was found; between giraffe and kudu in the 4th quarter ($r = 0.84$, $P < 0.01$, $n = 8$).

3.3.4. Foraging path comparisons

In *Acacia tortilis* savanna, the null hypothesis of the chi-square goodness of fit test (i.e. that there is no significant difference between foraging paths) was rejected for the following foraging path comparisons (Table 3.8): giraffe/impala, giraffe/steenbok, kudu/impala, kudu/steenbok, and impala/steenbok. The

Table 3.8. Results of foraging path comparisons in *Acacia tortilis* savanna[a].

Browser pairs	Woody plant species significantly more common in each foraging path, as isolated by 95% confidence limits	Chi-square statistics[b] $Ch(Test\ Y$
Giraffe + Kudu		16.08 10
Giraffe + Impala	*Acacia exuvialis*	38.35** 12
Giraffe + Steenbok	*Dichrostachys cinerea, Grewia monticola* *Securinega virosa*	47.78** 16
Kudu + Impala	*Acacia exuvialis*	26.3* 12
Kudu + Steenbok	*Dichrostachys cinerea Grewia flavescens, G. monticola* *Securinega virosa*	26.13** 8
Impala + Steenbok	*Dichrostachys cinerea, Grewia monticola, G. flavescens, Acacia exuvialis* *Securinega virosa*	65.49** 12

[a]Number of sampling stations per foraging path: giraffe, 124; kudu, 65; impala, 145; steenbok, 44. Number of records made over all sampling stations per foraging path: giraffe, 343; kudu, 170; impala, 335; steenbok, 105 (one record = one plant species marked present at a sampling station).
[b]Chi-square statistics calculated to test H_0: no difference between foraging paths of each browser pair.
*$P < 0.05$.
**$P < 0.005$.

foraging paths of giraffe and kudu were not significantly different ($0.1 < p < 0.05$).

Foraging paths in *Acacia tortilis* savanna were separated by a consistently high occurrence of *Securinega virosa* in the foraging path of steenbok, and *Acacia exuvialis* in that of impala (Table 3.8). Steenbok tended to avoid the *Dichrostachys cinerea / Grewia* spp. association, so that in all pairwise comparisons the 95% Bonferroni intervals isolated this association as being significantly more common in the foraging paths of other browsers.

In *A. nigrescens* savanna, a highly significant difference was detected between giraffe and kudu foraging paths ($Chi^2_{calc} = 127.8$, $Chi^2_{0.001,25} = 52.6$). This result is based on a sample size of 514 availability records from 180 sampling stations for giraffe, and 1022 availability records from 303 sampling stations for kudu.

The giraffe foraging path in *Acacia nigrescens* savanna was separated from that of kudu by higher proportions of occurrence of *Acacia nigrescens* and *A. tortilis*. The following shrub species were significantly more common in the kudu foraging path: *Securinega virosa*, *Ormocarpum trichocarpum*, and *Dichrostachys cinerea*.

3.4 DISCUSSION

3.4.1 Body size and habitat specialisation

The finding that diversity of habitat use increases *with increasing body size* was derived from a quantitative analysis of habitat use in three ruminant species across a wide body size range. While this is a small sample of species, the result is supported by patterns of habitat use documented for other ungulates endemic to the KNP (Smithers, 1983). For example klipspringer (*Oreotragus oreotragus*) and bushbuck (*Tragelaphus scriptus*) are both small ruminants (11 kg and 30 kg) with very specific habitat requirements; klipspringer are restricted to rocky outcrops and bushbuck to riparian thickets. Such habitat specificity is not shown by any larger ungulate.

I propose that a wider feeding tolerance in larger herbivores leads to the use of a wider range of habitat types (du Toit and Owen-Smith, *in press*). *This results* in a more even use of environmental resources, causing *population metabolism to scale positively with* species body mass. Being more evenly dispersed within *ecosystems*, larger herbivores are also less affected by local disturbances (such as fire or rainfall variations). Wider habitat use by larger species could be a common pattern among primary consumers as a

consequence of increased dietary tolerance for either a wider range in nutritional quality, or a wider range of food item sizes (May and MacArthur, 1972; Schoener, 1974a). A similar pattern could be expected among secondary consumers as a reflection of the tendency for predator and prey sizes to be related (Rosenzweig, 1966; Peters, 1983).

3.4.2 Body size and home range area

Comparing indices of home range is highly problematic because of the variety of methods used for home range estimation (Jennrich and Turner, 1969; Swihart *et al.*, 1988). Hence only general comparisons may be attempted between home range estimates derived for each species in this study and those from studies conducted elsewhere. This is particularly in view of the fact that it is only relatively recently that radio telemetry has come into common usage in African ungulate studies.

The giraffe estimate (282 km^2) is somewhat larger than the average home range areas reported for adult females from other studies. Estimates made by Leuthold and Leuthold (1978) in the Tsavo East National Park, Kenya, had a mean of 161 km^2 (range, 9-484 km^2). Pellew (1984c) found that adult females in the Serengeti also covered about 160 km^2, and that adult males covered

even less. This is in contrast to my finding that the mature male that I monitored using radio telemetry for a total period of one month, spaced over 3½ months, moved over a very much wider range than the female. Foster and Dagg (1972) reported a mean home range area of 85 km² for adult females in the Nairobi National Park, Kenya, and Berry (1978) reported an average area of 68 km² for adult females in the Luangwa valley, Zambia. In both cases these estimates were based on sightings of known animals within a fixed study area, and if animals moved outside of this they were not monitored. Langman (1973) used radio tracking in the Timbavati Nature Reserve, South Africa, and reported the very small mean home range area of 24.6 km² for adult females.

Owen-Smith's (1979) home range estimates for two kudu groups in the Nwamuriwa region of the Tshokwane study area (8.2 km² and 11.2 km²) match the estimate from this study (7.87 km²) for a group in the same area (K900, Table 3.2). Other home range estimates for kudu (based on field sightings and radio tracking) are from the Andries Vosloo Kudu Reserve in the Eastern Cape, where adult females covered an average area of only 1.27 km² (Allen-Rowlandson, 198(

The average home range area estimated for adult female impala in my study (5.81 km²) is very similar to that

(5 km²) found for adult females, non-territorial males and juveniles in the Serengeti (Jarman, 1970). However, Murray (1982), working in the Sengwa Wildlife Research Area in Zimbabwe, calculated the mean 90% home range area for adult females as a mere 0.6 km².

Previous to my study, reliable estimates of steenbok home range area have not been reported.

The above estimates for giraffe, kudu and impala show wide variations among the average areas that individuals of each species are reported to cover. This is no doubt due to ecological differences among study regions, and methodological differences among studies. For interspecific comparisons of home range area, such variations highlight the importance of using the same methods, in the same area, and during the same period, for individuals of all species concerned.

Home range area among browsers in the central KNP was closely related to body mass, and the slope of the log-log relationship (1.38) was not significantly different to that found by Swihart *et al.* (1988) for mammalian herbivores (1.55). These authors standardized the data used in their analysis by including only home ranges estimated by the MCP method from locational data collected by radio telemetry and direct observation. In the relationship for the KNP browsers, the lower 95%

confidence limit to the body mass exponent (1.01) confirms that home range area scales on body mass with an exponent significantly higher than that of metabolic rate (0.75). The exponent is also significantly higher than 1, a result inconsistent with the predictions of Lindstedt *et al.* (1986).

As discussed by Reiss (*1988*), *it remains to be* adequately explained why home range area should scale *on body mass with an exponent* that is consistently higher than 0.75. Schoener (1968) and Harestad and Bunnell (1979) suggested that home range area cannot scale in proportion to metabolic rate, because the probability of unproductive patches being included in the home range will increase with increasing home range area. Hence larger species have to cover increasingly more ground than would be expected if environmental productivity was spatially uniform. Damuth (1981*b*) countered this with evidence that productivity of the environment per unit area is no less for large species than it is for small (see also Damuth 1981*a*, 1987). In fact among certain mammalian herbivores it has now been found that large species actually extract *more* energy from community resources than smaller species do (see Brown and Maurer, 1986, for granivorous desert rodents; Owen-Smith, 1988, for African savanna ungulates).

Because home range sharing increases with body size,

Damuth proposed that among the larger species each individual has to cover increasingly more ground to encounter sufficient food for its *exclusive* use. This hypothesis assumes that home range area is mediated by intraspecific competition, which may be valid in certain circumstances, but I find it hard to credit among the animals I studied. For example, the average home range area of impala in a clan of over 200 animals was less than 6 km^2, while the average kudu cow group, which consisted of about 7 animals, moved over an area of 22 km^2.

The hypothesis proposed by Lindstedt *et al.* (1986) is that an animal sets the size of its home range to ensure adequate energy to last for the duration of critical biological time periods. This also fails to *explain the home range / body mass relationship among* browsers in the KNP. Firstly, the critical biological time period of lactation is synchronised (in impala and kudu) to occur at the start of, or during, the wet season when food is abundant. At this time kudu cows make short foraging excursions away from their calves, which are hidden in thickets, and to which the cows return regularly to nurse (personal observations). Secondly, Lindstedt *et al.* fail to take into account the rate at which food resources regenerate, enabling consumers to return and use feeding sites again (see also Reiss, 1988).

My data are not extensive enough to introduce a new hypothesis as to why animals have the home ranges that they do. I suggest, however, that the assumption upon which the above hypotheses are based requires testing. If animals cover the minimum area that they *have to* in order to feed themselves, then by Damuth's hypothesis, members of a herd will cover *less ground after* the herd's size is reduced. This could be easily tested on *buffalo herds in the KNP, for* example, by monitoring home range sizes before and after culling. I also *suggest* that the alternative hypothesis might offer more promise. That is, an animal will cover as much ground as it profitably *can*. A benefit of covering a large area is that this increases the probability of encountering dispersed patches of high quality foods (e.g. for a giraffe, patches of *Dichrostachys cinerea* in pod). Another benefit is the maintenance of familiarity with habitats that might be required during periods of resource shortage (e.g. for kudu, watercourses and riverlines). Deriving a predictive model based on the above assumption requires consideration of a variety of size-dependent variables, which in addition to metabolic rate would include the speed and energetics of locomotion (*Calder, 1982*; Pennycuick, 1979; Altmann, 1987).

3.4.3 Habitat selection

Two general patterns emerge from this analysis. Firstly, it is apparent that giraffe are generalists at the habitat level. No consistent preferences were found to prevail through the seasonal cycle, and instead giraffe moved between habitats in response to the availability of preferred phenophases in their food plants. In fact it was only in the late dry season and early wet season that proportional habitat use differed significantly from availability. Kudu were found to be rather more selective for particular habitats, favouring the hills and hillbase ecotone for most of the year. Steenbok were particularly selective, maintaining a consistently strong preference for *Acacia tortilis* savanna patches throughout the year. This pattern of increasing habitat selectivity with decreasing body size is consistent with the pattern of decreasing diversity of habitat use with decreasing body size, as described earlier.

The second general pattern is that of increased preference for habitats of the lower catena during the dry season. This was found to apply for giraffe, kudu, and impala. Steenbok were the exception.

Seasonal movement across the drainage catena has been documented before, for giraffe (Hall-Martin, 1974*b*;

Leuthold, 1978; Pellew, 1984*a,b*), kudu (Simpson, 1972), and impala (Jarman, 1972; Jarman and Sinclair, 1979). Similar movement patterns have also been described for grazers (Bell, 1970). The attraction of the lower catena is vegetation which remains green for longer into the dry season where the watertable is closest to the surface. Although kudu were found to favour the hills and hillbases as well as riverine habitats in the dry season, this is actually less of a spread across the catenary sequence than it may seem. There are numerous gullies and drainage sumps in the hills, and seepage zones occur where the hills meet the savanna. Steenbok are well adapted to dry conditions, and by feeding very selectively on food items with a sufficiently high preformed water content, they are able to remain on the upper catena throughout the year (see Chapter 4).

Over the range of browsers and habitats considered here, habitat preferences were found to overlap relatively little through the year. It is during the "lean" season that adaptations promoting niche separation are most strongly selected for, however (Schoener, 1986*a*), and for savanna ungulates the lean season is the late dry season. This is considered a nutritionally critical period for giraffe in the Transvaal lowveld (Hall-Martin, 1974*b*, 1975), and a marked drop in condition is evident at this time in

kudu (Brynard and Pienaar, 1960; Novellie, 1983; personal observations). Impala in the central KNP also lose condition in the dry season (personal observations), and severe population losses may occur if this period is prolonged (Walker *et al.*, 1987). However, it was during the dry season that giraffe, kudu, and impala were found to converge on comparatively small habitats of the lower catena. A similar dry season convergence has been reported for giraffe and lesser kudu (*Tragelaphus imberbis*) in riverlines of the Tsavo East National Park, Kenya (Leuthold, 1978). Hence it would seem that for the browsing ruminant guild at least, differential habitat selection is actually less important in promoting coexistence than previous studies (e.g. Lamprey, 1963) might suggest.

3.4.4 Foraging path selection

Comparisons between foraging paths of four syntopic browsing ruminants show that while woody plants occurring in one foraging path occur in others too, there may be significant differences between the relative proportions in which they occur. An analogy is to imagine that all woody plants in a habitat are marked on a map by dots of equal size but different colours for each species. If the various foraging paths were cut out in strips and laid side by side, they

would have visibly different colour tones.

It is to be expected that dietary differences would be responsible for "tonal" differences between foraging paths. In the case of steenbok this is clearly apparent. The foraging path of this species was separated from the others by a high proportional occurrence of *Securinega virosa*, which is the woody plant best represented in the steenbok diet (Chapter 4). The impala foraging path was separated from the others by *Acacia exuvialis* though, which is relatively poorly represented in the impala diet (Chapter 4). This apparent anomaly highlights the fact that only woody plants were recorded along the foraging path, while impala are mainly grazers for most of the year. I suggest that *A. exuvialis* occurs in association with certain sward characteristics that are selected by impala when grazing.

Although no difference was detected between the foraging paths of giraffe and kudu in *Acacia tortilis* savanna, a clear separation was evident in *A. nigrescens* savanna. In this habitat the giraffe foraging path was characterised by a high proportional occurrence of *Acacia* trees, with shrubs being more common in the foraging path of kudu. This separation is to be expected from the influence of body size on

differential accessibility of woody plant growth forms (Chapter 4).

Separation by microhabitat has been well documented for certain vertebrate groups such as *Anolis* lizards and birds (reviewed by Schoener, 1974a; Moermond, 1986). Granivorous desert rodents also separate by microhabitat (Brown, 1975) although this is considered unusual among terrestrial mammals due to their supposed inability to partition space vertically (Schoener, 1974a). This inability clearly does not apply to giraffe, however (see also Chapter 4), and horizontal overlap between other syntopic browser species is reduced by each moving between qualitatively different feeding sites. In Kyle National Park, Rhodesia, Ferrar and Walker (1974) found that discriminant function analysis separated large herbivores according to proportional abundance of trees, shrubs, and herbs at sites used by each species. Separation by these site characteristics was more marked than by physical habitat structure. For studies on spatial patterns of resource use by large herbivores, such findings demonstrate the importance of a spatial scale intermediate between the plant and the plant community. This scale must be defined by animal perceptions and foraging responses (Wiens, 1976; Senft *et al.*,1987), and for ungulate guilds I propose the foraging path as a suitable scale at which to investigate spatial

separation within habitats.

3.6 SUMMARY

The biotope of a large browsing ruminant (e.g. a giraffe) includes a relatively wide range of habitats. Wider habitat use by larger species is expected as a consequence of the allometric relationship between body size and gut capacity. This results in larger herbivores tolerating a wider range in diet quality, and hence metabolising a larger share of community resources. The ability of larger species to use a larger proportion of environmental productivity enables larger species to include a wider range of food patches in their home ranges. As has been found elsewhere, home range area scales with body mass according to an exponent (in this case 1.38) that is significantly higher than expected from metabolic requirements alone (i.e. 0.75). Current explanations are inadequate and require further investigation. Among the larger browsers (giraffe and kudu), it is in the dry season that certain habitats are used with significantly higher intensities than would be expected from availability. These habitats are those occurring low on the catenary drainage sequence.

The biotope of a small browsing ruminant (e.g. a steenbok) may occur entirely within one habitat (i.e. vegetation community). Small browsers tend to specialise on certain habitats which they use

throughout the seasonal cycle (short grass *Acacia* patches for steenbok, rocky outcrops for *klipspringer*, riverine thickets for bushbuck, etc.). Although this habitat specialisation may result in ecological separation by habitat for small browsing ruminant species, larger species overlap considerably in their habitat preferences, particularly in the dry season. Despite overlaps in habitat use, spatial overlaps in food resource use are reduced by syntopic species feeding along qualitatively different foraging paths.

CHAPTER 4

G PATTERNS

4.1 INTRODUCTION

In their recent review of African ungulate ecology, McNaughton and Georgiadis (1986) conclude that a principal factor contributing to resource partitioning is the ordering of syntopic species along a *browser-to-grazer continuum*. The distribution of species along this *continuum is uneven, however*, with grazers and browsers being clumped at either end. Of the 44 large herbivore species occurring in African savannas, 20 are classified as grazers, 13 as browsers and only 10 as mixed feeders (Owen-Smith, 1982).

Resource partitioning among species at the grazer end of the continuum has received more attention than among those at the browser end. This is largely due to a concentration of studies on ungulates of the Serengeti grasslands (see Sinclair and Norton-Griffiths, 1979). These studies have shown that grass is a heterogeneous food resource from which different grazer species select diets consisting of different proportions of leaf, sheath, and stem (Gwynne and Bell, 1968). Such trophic distinctions are related to *differences in body* size, digestive physiology and mouth structure (Bell, 1971; *Jarman, 1974; Jarman and Sinclair, 1979*; Demment and van Soest, 1983). It is expected that morphological *differences* should result in trophic distinctions between browsers in much the same way as between

grazers (Jarman, 1974), although this has not been investigated. In this chapter I consider resource partitioning among four syntopic browsing ruminant species of widely differing body size, and relate my findings to those of previous studies on the African grazing ungulate guild.

An important assumption underlying the concept of resource partitioning is what Moermond (1986) calls the "jack-of-all-trades" principle, in that the ability to perform well at some trades restricts the ability to do well at others. Applied to animals, differences in morphology and behaviour result in different abilities to use different resources and hence result in the potential to partition those resources. Measuring the degree to which consumers partition resources (in this chapter considered to be food) is problematic, however (Schoener, 1974a,b; Hurlbert, 1978; Lawlor, 1980; Moermond, 1986). Measures of overlap in proportional use of the same foods may be biased by the contributions of certain foods that are actually not limiting because they are abundant (Lawlor, 1980; Moermond, 1986). Overlap measures are nevertheless useful for identifying the potential for competition when most profitable foods *are* limiting, such as during the late dry season in African savannas (French, 1985; Hansen *et al.*, 1985). Alternatively, measures of trophic similarity that are independent of food

abundance may reflect evolutionary divergence due to past competitive pressures (Lawlor, 1980). Such measures are based on comparisons of electivities (feeding preferences).

A two-pronged approach is adopted in this chapter. Firstly I consider the food resource base by analysing diet composition in each study species, and investigating the influence of seasonality on diet composition, diversity and overlap between species. Secondly I consider partitioning of the food resource base by comparing feeding preferences, and investigating the factors that influence feeding preference in each species. These include both plant factors (chemistry and accessibility) and animal factors (body size and dietary tolerance).

4.1.1 The food resource base

4.1.1.1 *Diet composition*

By Root's (1967) definition, food resources and the ways in which they are used define the guild. Strictly speaking, the guild cannot be defined *a priori* (Jaksic, 1981), but this makes it difficult to decide which species to include in a guild study in the first place. The way around this is to include syntopic species on the basis of existing knowledge.

Previous studies on the diets of giraffe (Innis, 1958; Foster, 1966; Foster and Dagg, 1972; Leuthold and Leuthold, 1972; Oates, 1973; Hall-Martin, 1974*a*,*b*; Hall-Martin and Basson, 1975; Leuthold and Leuthold, 1978; Pellew, 1984*a*,*b*), kudu (Wilson, 1965, 1970; Conybeare 1975; Owen-Smith, 1979; Novellie, 1983; Cooper, 1985; Owen-Smith and Cooper, 1985), impala (Jarman, 1971; Rodgers, 1976; Jarman and Sinclair, 1979; Dunham, 1980; Monro, 1980; Fairall, 1983; Cooper, 1985; Owen-Smith and Cooper, 1985) and steenbok (Huntley, 1972; Cohen, 1976; Smithers, 1983) show that these four species all depend to a large degree on dicotyledonous plants for their food requirements. In the case of impala this is mainly during the dry season. Most of the studies cited above were single-species studies conducted in various parts of Africa (East Africa, South Africa, and Zimbabwe) over different time periods and using different methods. Trophic interactions within a guild can only be accurately assessed from dietary comparisons between a representative range of species that have been studied *in the same area, at the same time,* and in the same way (Hansen *et al.*, 1985). These conditions have been adequately met for grazing ungulates in the Serengeti (Bell, 1970, 1971; Jarman and Sinclair, 1979), but not previously for savanna browsers. This section is a contribution towards filling that gap. The food

resource base used by four syntopic browsing ruminants is described, and the inclusion of these species in the same guild study is defended.

4.1.1.2 *Seasonality and diet overlap*

In seasonal environments, Schoener (1982, 1986a) hypothesises that feeding specialisations that result in niche separation should be selected for most strongly during the "lean" season, when resources are most limiting. Feeding constraints should be relaxed during the "fat" season when profitable foods that are abundant may be converged upon by more species. Here I test this hypothesis on the seasonal feeding patterns of browsing ruminants in the central KNP.

Seasonality in southern African savanna vegetation results from a highly seasonal rainfall pattern. Almost all (86%) of the mean annual rainfall in the Tshokwane region of the central KNP (590 mm) falls between October and March (data from Gertenbach, 1980). Consequently there is a long dry season during which soil moisture is lost, mainly by evaporation from the soil and transpiration (Whitmore, 1971). This is reflected in a progressive decline in abundance of green foliage as plants in the herb layer wilt and either die or become dormant, and many woody plants shed their leaves.

The soil-plant-herbivore sequence of rainfall effects imposes a lag period between rainfall and dietary response among browsing ungulates as measured in terms of diet composition. Further, the tendency for some ungulates to move down the catenary sequence in the dry season (Chapter 3) effectively extends the wet season diet by allowing access to green foliage in the hollows when the hills are brown (see also Bell, 1970). Hence in years of normal rainfall it is the late dry season (July-October) that is the lean season, and this is when declining condition is evident in giraffe, kudu and impala (Brynard and Pienaar, 1960; Hall-Martin, 1974a; personal observations).

Jarman (1971) found that dietary overlap between ungulate species in the Zambezi Valley was high during the wet season, declined somewhat in the early dry season when food "refuges" were resorted to, and increased again in the late dry season when food resources were most limiting. In the eastern Transvaal lowveld, Hall-Martin (1974b) found that giraffe in the dry season fell back on food reserves (*Colophospermum mopane* and evergreens in riverine thickets) that were seldom used at other times. In this section I consider such seasonal variations in feeding patterns among browsing ruminants in the central KNP. I investigate the use of dry season food reserves, and test the

hypothesis that dietary diversity and overlap are *reduced during* the lean season.

4.1.2 Partitioning of the food resource base

4.1.2.1 *Differences in feeding preferences*

Implicit in the jack-of-all-trades principle (*Hoermond*, 1986) is the assumption that differences in resource use patterns will result from differences in (a) morphology and (b) behaviour patterns that influence the *way morphological* features are used (see also Schoener, 1974*a*). Among food resource use patterns, such differences are best investigated by comparing "electivities" (Schoener, *1974b*), *which* best reflect the evolutionary consequences of past competitive pressures (Lawlor, 1980).

Electivity is the expression used for Ivlev's (1961) measure of preference. Here I use an index of feeding preference for woody plants (based on Ivlev's index) in a formulation to *estimate similarities* between the browsing patterns of four syntopic ruminant species. These estimates of similarity are used to assess the potential for competition between species pairs, and to monitor convergence and divergence of diet selection patterns between wet ("fat") and dry ("lean") seasons. Factors affecting feeding preferences (and hence

similarities between species) are considered in the sections that follow.

4.1.2.2 *Feeding preference and plant chemistry*

By definition, the average diet of a selective herbivore is of a higher quality than the average quality of available food in the habitat as a whole (McNaughton and Georgiadis, 1986). The process of diet selection may thus be considered as the means by which diet quality is enhanced to a greater or lesser degree above a certain background level specific to each habitat. Quality of forage to ungulates varies according to its proportional composition of quality enhancers and quality reducers. The former are nutrients and the latter include fibre and plant secondary metabolites, which are either digestion inhibitors or toxins.

One school of thought considers maximizing the intake of nutrients to be the most important basis upon which diet selection operates (Westoby, 1974; Belovsky, 1978, 1981), and among grazers there is good evidence for this (Crawley, 1983; Belovsky, 1986). Another school of thought considers minimizing the intake of secondary defence compounds to be more important (Freeland and Janzen, 1974; Rosenthal and Janzen, 1979; Bryant and Kuropat, 1980; Bryant *et al.*, 1985). This second

hypothesis is particularly applicable to browsers as chemical defences against herbivory appear to be more developed among dicotyledons, especially woody species, than among grasses (Rhoades and Cates, 1976; Malechek and Balph, 1987). In particular, the level of tannins in woody browse has been recently found to have a strong negative influence on ruminant feeding preference (reviewed by Malechek and Balph, 1987). Reasons for this could be a combination of (a) *inhibition of* protein digestion (van Hoven, 1984; Robbins *et al.*, 1987*a*), (b) inhibition of cell wall digestion (Cooper and *Owen-Smith*, 1985; Barry and Blaney, 1987; but see Robbins *et al.*, 1987*b*), and (c) taste repulsion (Provenza and Malechek, *1984*). A *third* hypothesis (Cooper *et al.*, 1988) arises from recent findings on the feeding responses of browsing ruminants to seasonal variations in woody plant chemistry, in a South African dystrophic savanna (Nylsvley Nature Reserve, northern Transvaal). These findings suggest that plants with a relatively high condensed tannin content are acceptable to browsers if the protein content is also high. Hence large browsers may not necessarily select their diets according to levels of either nutrients or secondary metabolites, but according to the balance between the two.

Rigorous testing of the above hypotheses requires intensive research beyond the scope of this study.

Plant chemistry analyses were nevertheless performed on a randomly chosen sample of woody plants that are common in the central KNP, and for which the feeding preferences of four indigenous browsing ruminant species were estimated. In this section I use these analyses to investigate the relationship between feeding preference and plant chemistry among browsing ruminants over a wide body size range.

4.1.2.3 *Feeding preference and forage accessibility*

Rate of harvest is considered to have an important influence on the feeding preferences of large herbivores (Bolovsky, 1978; Maschek and Balph, 1987). For browsing ruminants this rate is constrained by structural plant features such as spinescence and twiggy growth form (Dunham, 1980; Owen-Smith, 1982; Cooper and Owen-Smith, 1986), and perhaps canopy architecture in trees (Foster and Dagg, 1972). Such features impede access to edible plant parts within the feeding height range of any particular browser. Hence it might be predicted that structurally defended plant phenotypes will be relatively less preferred food plants to browsers. However, this prediction has to be balanced against (a) the nutritional quality of the forage that browsers are able to harvest from such plants, and (b) the ability of browsers to adapt their feeding techniques to overcome structural defences.

Pellew (1984a) found that leaves and shoots of thorned browse plants used by giraffe were particularly nutritious. Furthermore, while giraffe took smaller bites from thorned *Acacia* species than from thornless shrubs, this was compensated for by increased bite rates (Pellew, 1984b). On the other hand Cooper and Owen-Smith (1986) found that spinescence was effective in reducing leaf and shoot losses to below the levels *expected for* equally palatable but non-spinescent species, when fed on by kudu, impala and goats.

The ultimate woody plant feature *influencing browser* accessibility is the height at which palatable parts occur above ground. While steenbok and impala have limited access to foliage on low branches that are readily accessible to kudu, giraffe have exclusive access to the upper canopies of many mature trees. Use of different feeding levels in the vegetation is a standard explanation for coexistence among African browsing ungulates (Lamprey, 1963; Leuthold, 1978; McNaughton and Georgiadis, 1986). This hypothesis has not been tested however, and although it is obvious that large browsers can eat food that smaller browsers cannot reach, it is less obvious why large browsers do not also eat food that smaller browsers *can* reach. I *suggest* that the *larger* of two *syntopic* browsers would usually feed at a higher level than the other as this imparts a relative advantage in locating unbrowsed

protein-rich shoot tips (see also Pellew, 1984a). If this is so, then giraffe should usually feed at a higher level than kudu, and giraffe bulls (being taller) should feed at a higher level than cows.

Here I consider the influence of plant structural features on feeding preferences of browsing ruminants of differing body size, and test the hypothesis that feeding height stratification promotes resource partitioning between syntopic species.

4.1.2.4 *Feeding preference and dietary tolerance*

The Jarman-Bell principle is based on the African ungulate studies of Jarman (1971, 1972) and Bell (1970, 1971), and was formalised by Geist (1974:206) as follows:

> *"The body size and population biomass of ungulate species is a function of the fiber content (digestibility) and density of the forage they exploit."*

This principle is explained in terms of the allometric scaling of metabolic rate. The smaller the animal the higher its mass-specific metabolic rate, and so the higher the quality (digestibility) of food it requires. High quality food items are relatively rare and

dispersed, so it is expected that only small animals can harvest sufficient high quality food items to meet their metabolic requirements. Geist suggests that these include fruits, seeds, flowers and sprouting shoots, and because the biomass of these items is relatively small, the total biomass of small ungulates in a community should also be relatively small. Larger herbivores have higher absolute energy costs, and because high quality food items are too rare to satisfy their energy demands, they are forced to expand their diets to include lower quality, more abundant plant material (Bell, 1971; Geist, 1974; Jarman, 1974; McNaughton and Georgiadis, 1986).

The Jarman-Bell principle appears to be widely applicable to African ungulates. Firstly, its predictions are closely matched by the feeding patterns of grazers, upon which the principle is essentially based (see Gwynne and Bell, 1968; Bell, 1970, 1971). Further, Jarman (1974) expanded on his earlier work by classifying African antelope (across the grazer-to-browser continuum) into five feeding styles, and found relationships between these and (a) body size and (b) social organisation. By this classification, species which feed very selectively on discrete food items tend to be small and solitary, while relatively unselective feeders tend to be large, wide-ranging and gregarious. Finally, in terms of population biomass it is the large

roughage feeders that generally dominate African ungulate communities (Cumming, 1982; Lawton and MacGarvin, 1986; Owen-Smith, 1988).

Despite the wide applicability of the Jarman-Bell principle, there is at least one species of African ungulate with which it has difficulty. This is the giraffe, which Jarman (1974) excluded from his feeding style classification as it is not an antelope. Giraffe are larger than all other ruminants but are capable of feeding very selectively on young shoots, pods and flowers (Hall-Martin, 1974*a*; Pellew, 1984*a*). Here I examine this apparent anomaly by comparing the feeding patterns of giraffe with those of smaller browsing ruminants in the central KNP. On the basis of this analysis, I suggest a revision of Geist's (1974) statement of the Jarman-Bell principle to make it more widely applicable to ungulates across the grazer-to-browser continuum.

4.2 METHODS

4.2.1 Feeding observations

Radio telemetry was used to locate marked individuals within each study population (according to the methods outlined in the previous chapter), enabling feeding observations to be made in habitats selected by these animals during each phase of the seasonal cycle. This avoided the problem of bias in favour of habitats in which animals are most easily located by eye. Only one habitat within the study area was inaccessible and this was the hills habitat, consisting of Nwamuriwa and Nwamuriwane hills, both of which have steep and roc slopes. Of the study animals, only kudu made use of this habitat, which was included in the areas covered by two out of the four cow groups which constituted the kudu study population.

Once located, observations were made on collared or otherwise easily identifiable individuals of each study species, using the continuous focal-animal method (Altmann, 1974). Observations were made from a 4-wheel-drive vehicle, using 7 x 50 binoculars at distances from 2-20 m. Animals within the study area were habituated to vehicles, apart from which they were completely uninfluenced by humans and their movements

were not restricted by any unnatural barriers. This situation well satisfied the requirement for both internal and external validity of behavioural data collected by observation (Altmann, 1974).

During each observation period the focal animal was followed by driving slowly behind it, keeping as closely as possible to its foraging path. This was to measure distance moved (using the vehicle odometer) as well as make close inspections of feeding sites when necessary. Observation periods were of variable length, but usually varied between three and five hours depending on conditions. Termination of each observation period occurred either at a pre-determined time or else due to unforeseen causes. These included disturbance by predators (usually lion, *Panthera leo*, but also leopard, *P. pardus*, and spotted hyena, *Crocuta crocuta*), the onset of heavy rain which obscured visibility, mechanical problems with the vehicle, etc. Observation periods were pre-planned for each study species to include all the hours of the day between dawn and dusk for each month of the year.

4.2.2 Data capture

A portable microcomputer (Sharp PC-1500) equipped with 8K RAM was used for real-time recording of field observations. This type of computerised data capture

system is superior to the traditional check sheet method which is cumbersome, time-consuming, and error-prone, particularly when data ultimately have to be transcribed manually to a computer file (see Whiten and Barton, 1988). The use of portable microcomputers in the field is a relatively new development in biological research methodology, but is proving to be increasingly popular as its merits become realised (Demment and Greenwood, 1987; Unwin and Martin, 1987; Whiten and Barton, 1988). Because of the novelty of the particular method employed in this study, I describe it in some detail.

The Sharp PC-1500 was affixed to a clipboard which could be clipped to the vehicle dashboard, between the steering wheel and instrument panel. This enabled operation of the microcomputer with one hand while the other was used for steering or holding binoculars. Software was written in BASIC by the Quantitative Biologist for National Parks Board (P. Retief) according to the requirements of this project. Data entry was prompt-driven, ensuring consistency in data capture, and each accepted entry was acknowledged with an audio cue (i.e. a "bleep"). If an entry did not fit the demands of the prompt (e.g. an alphabetic character instead of a numeric) then the "bleep" would be of a higher pitch, and the entry would not be accepted. Prompts were programmed to appear on the display

(single line, 26 character width, liquid crystal) directly above special function keys (of which there were six) positioned in a row beneath the display. Each prompt option could thus be selected by pressing the special function key directly below it.

Each observation period began by entering an initiation line in which the species, sex, identification code, and age class of the animal were recorded together with a grid reference of map position (on a 1:100,000 map), habitat code, and the size of the group within which the focal animal was located. The date (by month and day) and time (by hour, minute, and second) of the initiation were entered automatically by the computer from its internal clock. After entering the initiation line, a main menu would appear on the display. This menu consisted of a series of prompt options relating to first order activity classes. These were "Feeding", "Moving", "Standing", "Lying", and "Obscured". The observation period would then progress by selecting from this menu, which directed the observer through a sequence of lower order categories within each activity class. Lower order categories within the feeding activity class will be described below (activities other than feeding were also recorded but are not included in this thesis). The observation period was terminated by entering a termination line in which the grid reference of map position was recorded, together

with distance moved (to the nearest 50 metres) as read off the vehicle odometer. The time at which the termination took place (in hours, minutes, and seconds) was entered automatically from the computer's internal clock.

The duration of a feeding event was the period between when a focal animal commenced feeding at a feeding station and when it swallowed the last mouthful at that station (unless feeding was abruptly terminated, e.g. due to alarm). A feeding station consisted of forage immediately available to the animal during the course of an uninterrupted feeding event (the features that describe a feeding event will be outlined shortly). This definition of a feeding station is similar to that of Novellie (1978) and McNaughton (1987), except that here it does not only apply when the focal animal's legs are stationary. While feeding on a patch of herbaceous (i.e. non-woody) forage, study animals would often move slowly through the patch with the head down, feeding continuously. This was considered to be an uninterrupted feeding event even if the head was raised briefly to look around while chewing.

The commencement of a feeding event was recorded by selecting the "Feeding" option from the main menu of first order activity classes on the microcomputer display. This would result in the instantaneous storage

of an event marker (which in this case would appear as an "F" in the printout) together with a time-stamp (in chronological time, denoted by hour, minute, and second). All following information would be appended on the same line thereafter. A second order menu would now appear on the display, consisting of four option prompts relating to height of feeding above the ground. Feeding height was categorised into four classes for all four study animals, and since these differed so widely in body size, the only possible method was to use the angle subtended by the *neck relative* to the forelegs. The four height classes included those *feeding heights corresponding* to neck angles closest to 45°, 90°, 135°, and 180° respectively. Neck angles were calibrated with height measurements for each species by separately measuring the height above ground of vegetation browsed within each neck angle class, using a tape measure weighted at one end with a plumb-bob. The browsing heights corresponding to each neck angle class are shown in Table 4.1.

After entering neck angle, the next menu to appear on the display consisted of option prompts relating to the plant growth form being fed on. These options were "Grass", "Forb", "Creeper", "Shrub", "Sapling", or "Tree". "Grass" consisted of all graminoids, and "Forb" all upright soft-stemmed dicots. "Creeper" consisted of sessile or attached soft-stemmed dicots, growing either

Table 4.1. Feeding height classes corresponding to neck angles*.

Neck angle	Class limit	Height of mouth above ground (m)			
		Giraffe	Kudu	Impala	Steenbok
45°	lower	0	0	0	0
	upper	1.7	0.7	0.4	0.25
90°	lower	1.8	0.8	0.41	0.26
	upper	2.7	1.1	0.7	0.4
135°	lower	2.8	1.2	0.71	0.41
	upper	3.7	1.7	1.15	0.6
180°	lower	3.8	1.8	1.16	0.6
	upper	4.5	2.0	1.45	0.9

*Subtended by the neck relative to the forelegs, in adult females of each species.

within the herbaceous layer or else entwined within the woody layer. "Shrubs" were classified as woody-stemmed bushy plants less than 2 m in height, usually with multiple stems. This class included woody stemmed vines. "Saplings" included the immature growth stages of woody plants, ranging from seedlings growing within the herbaceous layer to immature shrubs and trees less than 2 m in height. "Trees" were classified as large woody plants usually with single stems and growing above 2 m in height.

If "Grass", "Forb", or "Creeper" options were selected, then the programme would store a code to this effect (appearing as "1", "2", or "3" in the printout) after the time-stamp for that *feeding event*, and return to the main menu of first order activity classes. For herbaceous plants, plant part and species fed on were usually impossible to identify by observation through binoculars from a vehicle. This was because individual mouthfuls (especially in the case of kudu) often included a mix of plant parts removed from a patch of herbaceous plants made up of a variety of species. Even close examination of feeding sites on foot would not have solved the problem, since forbs were often bitten off at ground level, or even pulled out completely when the soil was soft after rains. Further, the study animals would all take flight immediately at the sight of a human outside of a vehicle. These problems did not

apply if the focal animal was feeding on a woody plant so that if "Shrub", "Sapling", or "Tree" were selected, the feeding event would be described further in terms of plant part and plant species.

For woody plants the plant part menu consisted of "Leaf", "Shoot", "Fruit", or "Flower" prompt options. "Leaf" referred to leaves that were individually plucked or else stripped off the stem, while "Shoot" referred to a mixture of leaves and the soft stems of terminal branchlets that were bitten off together. "Fruit" referred to soft fruits such as berries or drupes, as well as pods. "Flower" included all forms of inflorescence that were fed on. After selecting the required plant part option, a final menu was displayed for entry of the plant species being fed on. The menu consisted of prompts for the six most commonly used species, or alternatively a numeric code (ranging from 1-99) could be entered to denote any other species. A list of woody species with their numeric codes was immediately accessible in a plasticised flip-booklet affixed to the same clipboard as the microcomputer.

After recording the plant species being fed on, the woody plant species sub-menu would remain displayed. This was so that those woody plant species immediately available to the feeding animal (within a 5 m radius of the mouth) could be recorded during every fifth woody

plant feeding event. In the printout, codes for these species would appear separately from the code of the species being fed on. The reason (relevant to this chapter) for recording plant species available to a browser while feeding in a particular habitat was so that a measure of feeding preference could be derived (as will be described later in this methods section).

At the termination of a feeding event (indicated by the commencement of a new activity, e.g. walking, standing alert, or switching to a new forage type) the first order activity class relevant to the new activity would be entered immediately. If the focal animal became obscured behind other animals or vegetation, then the "Obscured" option on the main menu was selected. After manoeuvering the vehicle as quickly as possible into a position from which observations could resume, the activity in which the animal was engaged at the time would be immediately recorded. Time elapsed while the focal animal was obscured was dropped from subsequent analyses. This accounted for less than 1% of the total observation time recorded during the study period. If the focal animal crossed a habitat boundary, the observation would be terminated and a new one initiated in the new habitat. This practice resulted in a string of time-stamped events ordered in real-time sequence, bracketed between initiation and termination lines. The time taken to enter the required information for each

feeding event was minimised by the use of special function keys which each executed a number of functions at once. A trial exercise revealed that all the prompts requesting information on a woody plant feeding event could be answered within 3 seconds. For an herbaceous feeding event this time was even less. The mean durations of feeding events for giraffe, kudu, impala, and steenbok were 78, 60, 45, and 50 seconds respectively.

By use of the above method a total of 1,094 hours of focal animal observations were recorded during the study period, over a total foraging path distance of 631 km. A breakdown of hours recorded per study species during each quarter of the year is shown in Table 4.2.

4.2.3 Data storage

The 8 K RAM in the Sharp PC-1500 was sufficient to accomodate the software and at least five hours of continuous data capture. A feature of the software was a memory gauge that could be accessed at any time to indicate the percentage of memory that was no longer available, so that memory space was not over-run. At the end of each day of fieldwork, all data in the microcomputer were transferred to cassette tape. This cheap and convenient medium was found ideal for temporary data storage and backup in the field. A

Table 4.2. Hours of field observation data recorded during each quarter of the calendar year.

Quarter*	Hours recorded				
	Giraffe	Kudu	Impala	Steenbok	Total
1/4	62.7	69.8	38.8	57.4	229
2/4	46.5	60.9	33.2	43	184
3/4	79.5	98.5	65.1	45.7	289
4/4	118	152	70.1	52.4	392
Total	307	381	207	198	1094

*1/4, January-March; 2/4, April-June; 3/4, July-September; 4/4, October-December.

printout of the day's data was also obtained, using the Sharp CE-150 printer/cassette interface, which uses an X and Y axes plotter system on a 58 mm wide paper roll. Editing comments (e.g. correcting plant species codes) were transcribed by hand from a field notebook onto this printout, using the time-stamps as a reference. This annotated hardcopy was stapled to the relevant page of a "page-a-day" diary which was kept as a daily log of completed fieldwork. The data in the microcomputer were then erased in preparation for the next day of fieldwork.

Field data were stored by use of the above method for periods of between one and two weeks, before being transferred to a minicomputer at the KNP headquarters at Skukuza.

4.2.4 Data transfer and analysis

Data files stored on cassette tape in the field were transferred to the minicomputer (DEC PDP 11/73) by use of a Sharp RS-232 interface. This minicomputer operated under the UNIX operating system. Data files were checked on the screen and edited according to the editing comments made on each day's printout (using the UNIX text-editor "vi"). The data files were then stored on floppy diskette and backed up on hard disk. These edited data files were subsequently run through two

programmes (written in the programming language "awk" by the Quantitative Biologist for National Parks Board, P. Retief), which created two databases in the format required by the "Prelude" database package (VenturCom Inc., 1984). One programme created an activity database consisting of all events recorded over all activity classes. The other programme created a feeding database consisting only of feeding events.

The activity database consisted of 11 variables describing each observation. These were month, day, hour, animal species, animal i.d. code, sex, group size, habitat, first order activity, second order activity, and elapsed time. Elapsed time was in seconds, and for each observation this time was the difference between the time-stamp of that entry and the next. The feeding data-base consisted of 13 variables describing each observation. These were month, day, hour, animal species, animal i.d. code, sex, age class, habitat, neck angle class, plant growth form, plant species, and elapsed time. The elapsed time value for an observation in this database was identical to the value for the same feeding observation in the activity database.

As more data were collected, additional observations were appended to the above two databases which were sorted chronologically by month, day, and hour.

Temporary databases for each browser species were created using "Prelude" commands, selecting data out of the permanent databases by the animal species variable. Programmes made up of "Prelude" commands were used for descriptive analysis of these databases during the study period. Upon completion of the fieldwork phase of the study, both activity and feeding databases were converted into SAS format (SAS Institute Inc., 1985a), for statistical analysis on the mainframe computer at the University of the Witwatersrand.

4.2.5 Diet composition

An analysis of diet composition requires the identification of dietary components, so that the proportional contribution of each may be measured. Here dietary components are considered to be *forage types*. A forage type is defined as *a class of food items for which there may be assumed to be less variability in quality within the class* than between classes. In this broad definition food quality is assumed to vary as a function of the quantity of assimilable nutrients that can be ingested per unit time. This is dependent upon a range of features of the food resource operating either independently or in concert, of which the following are probably most important: digestibility (as influenced by content of fibre or digestibility-reducing phytochemicals such as tannins); content of specific

inorganic nutrients (such as phosphorus); toxicity (as determined by content of toxic phytochemicals such as alkaloids); feeding repellence (caused by the astringent taste of many phytochemicals); and structure (as exhibited by growth form, leaf size, spinescence, etc.).

Herbaceous forage types were categorised into three physiognomic classes: grasses, forbs, and creepers. Woody forage types were classified by plant species and and three categories of plant part: foliage (including "leaf" and "shoot"), fruit, and flower. This treatment considers different parts of the same woody plant to be distinct forage types, in contrast to early studies that analysed the diet simply in terms of "food plants" (for giraffe examples see Innis, 1958; Leuthold and Leuthold, 1972). The successively detailed classification of graminoid, non-graminoid herbaceous, and woody forage types follows the respective order of increasing complexity in anti-herbivore defence mechanisms displayed by these plant groups (reviewed by Malechek and Balph, 1987).

Diet composition was measured in terms of the proportional distribution of feeding time between forage types. For browsing ungulates, feeding time is a more accurate measure of quantity of food ingested than bite frequency (see Owen-Smith, 1979). This is because

of wide variations in bite size between forage types, as well as the obvious difficulty in counting bites taken by animals in the wild. Alternative methods include the "feeding record" method (Leuthold, 1971; Leuthold and Leuthold, 1972) in which feeding events on each plant species are counted without regard for relative feeding time allocation or plant part differentiation. This relatively crude method can be used to indicate feeding time allocation if records are made at regular time intervals (i.e. point sampling). Sampling time is then greatly reduced, however, especially for small browsers like steenbok which spend a relatively small proportion of the day feeding. Rumen content analysis is another popular method for estimating diet composition (Dunham, 1980; Hall-Martin, 1974a; Wilson, 1965; Smithers, 1983) but was ruled out in this study mainly because of its destructive implications but also due to the problem of differential digestibility of ingested forage types (Gaare *et al.*, 1977; Hanley *et al.*, 1985). The differential digestibility problem is even more pronounced in the final alternative, faecal analysis, which has nevertheless been used in other studies to estimate diet composition in African ungulates (e.g. Hansen *et al.*, 1985).

4.2.6 Seasonality

The relationship between proportional allocation of feeding time to each major dietary component (grass, forbs, woody plant foliage, fruits and flowers) and rainfall was investigated using simple linear correlation analysis. Four rainfall statistics were used: total rainfall (mm) for each month during which feeding data were collected for each study species; 2-month running mean of rainfall (2-MRMR), calculated as rainfall averaged over the month in question and the preceding month; 3-MRMR (averaged over the month in question and the preceding 2 months); and 4-MRMR (averaged over the month in question and the preceding 3 months).

Seasonal movement across the drainage catena was investigated for giraffe, kudu and impala. The monthly percentages of collared animal sightings made in riverine vegetation were plotted against rainfall statistics (see above) for each month.

4.2.7 Diet overlap

Diet overlap between a pair of browser species was assessed by two methods:

i. Percentage similarity

The percentage similarity coefficient (Brower and Zar, 1977; Pielou, 1977) was used to indicate the percentage of two diets that were identical. Percentage similarity (*PS*) is equivalent to percentage overlap, and is commonly used to indicate the similarity between two plant communities in terms of species composition (Goodall, 1978). The use of *PS* in animal ecology was demonstrated by Schoener (1970) who used it to measure percentage spatial overlap between habitat use patterns of *Anolis* lizards. Here *PS* was calculated over each quarter of the seasonal cycle, as well as the complete seasonal cycle, for each combination of diet pairs (*i.e. giraffe/kudu, giraffe/impala, giraffe/steenbok,* kudu/impala, kudu/steenbok, and impala/steenbok), by the formula:

$$PS = \Sigma \text{ lowest } [a_i, b_i],$$

where a_i and b_i denote the percentage allocation of feeding time to the ith forage type by browsers *A* and *B* respectively. *PS* is given by the sum of all the lowest values from each pair of percentages.

ii. Correlation analysis

The Pearson product-moment method of correlation

analysis (SAS Institute Inc., 1985a) was used to estimate the strength of the relationship between diet composition in one browser species and another, during the same phase of the seasonal cycle. Correlation analysis was performed (for each quarter of the year and each combination of diet pairs) on percentage feeding time distribution among (1) all forage types, (2) all browse forage types (i.e. excluding grass), and (3) all woody browse forage types (i.e. excluding all herbaceous forage types). The same analyses were also performed on mean annual diets. A correlation was considered significant if $P < 0.05$. When certain forage types (e.g. grass or all herbs) were excluded, then the percentage contribution of each remaining forage type was scaled up so that the sum of all percentages was always 100.

A combined measure of the overall correlation between the diets of all browsers during each seasonal quarter was obtained by fitting a two-way analysis of variance model (forage types x browser species, one observation per cell) to each data set (i.e. all forage types; no grass; no herbs). Output of the SAS ANOVA procedure (SAS Institute Inc., 1985b) includes a coefficient of multiple determination, R^2, which measures how much variation in the dependent variable (percentage dietary contribution) can be accounted for by the model. The larger the R^2 value, the better the model fits the

data. The multiple correlation coefficient, R, is the positive square root of R^2, and ranges for 0 to 1. The larger the value of R, the closer the overall correlation between the diets of all four browsers.

4.2.8 Dietary diversity

The Shannon-Wiener diversity index H' (Shannon and Weaver, 1949; Pielou, 1977) was used as a measure of the diversity of (a) the mean annual diet, and (b) the diet during each month of the year for each browser species by the formula:

$$H' = -\Sigma\, p_i \log p_i,$$

where p_i is the proportion of feeding time allocated to the ith forage type included in the diet (see section 4.2.5 for the definition of a forage type). Justification for the use of the Shannon-Wiener index as a measure of diversity in ecological studies was presented in Chapter 3.

Note that the measurement of dietary diversity is strongly influenced by the way in which dietary components are classified. Some authors have compared diets in terms of species richness (e.g. Hansen *et al.*, 1985). A serious drawback to this is the underestimation of additional diversity within species

(particularly woody plants), contributed by nutritionally diverse plant parts (shoots, leaves, fruits, flowers, etc.). On the other hand, overestimation of dietary diversity would result from quantifying grass species richness in the diet of impala for example, which may select one main forage type (green leaf) from a sward made up of numerous palatable species (see also Jarman and Sinclair, 1979). The approach taken here, using forage types rather than plant species, attempts to strike a balance so that dietary diversity may be measured more meaningfully.

4.2.9 Feeding preference

The preference of a consumer for a particular component may be defined as *"a reflection of the likelihood of that component being chosen if offered on an equal basis with others."* (Johnson, 1980:66). The measurement of preference thus requires a comparison of usage and availability of each component, and is expressed as an index. In this study, usage of food components by study animals was measured as the proportion of feeding time allocated to that component. Availability was measured as the proportional frequency of occurrence of that component along the animal's foraging path. Only the availability of woody plants was considered, since herbaceous plants are difficult to identify without close inspection, and are often obscured by other

plants. Species of woody plant (of all growth forms) occurring within a 5 m radius of the focal animal's mouth were recorded during every fifth woody plant feeding event. If, however, a woody plant (e.g. a large tree) within this 5 m radius did not bear foliage within the feeding height range of the focal animal, then it was not recorded as present. The list of species recorded as present included the species being fed on at the time of sampling.

The use of a sampling area of 5 m radius at every fifth woody plant feeding station was so as to obtain suitable samples of immediately available woody browse species, with independence between sampling stations (see previous chapter). This method of *availability* sampling is analogous to quadrat sampling along the foraging path, using a quadrat area of approximately 80 m^2. Availability of woody browse was recorded in terms of species present, and not biomass, since quick biomass estimations are impossible to make and in any event browsers use only a fraction of the standing crop of browse at a feeding station before moving on. Further, in heterogeneous plant communities, quantitative measures add little useful information to that yielded by a simple species list for each quadrat (Goodall, 1978; Pielou, 1984).

The proportional occurrence of a woody plant species in

the foraging path of a particular species of study animal (pr_p) was calculated as $pr_p = n_i/N$, where n_i is the number of times that the ith woody plant species was recorded as present over all sampling stations, and $N = \Sigma n_i$. The proportional use of a woody plant species was calculated as the proportion of woody plant feeding time (pr_t) allocated to feeding on that plant species. The feeding preference index (*FPI*) for a particular woody plant species was calculated as:

$$FPI = pr_t/pr_p.$$

This ratio of usage and availability is mathematically identical to Ivlev's forage ratio (Ivlev, 1961). By this ratio, a food item is considered preferred when the ratio value exceeds 1, and for ungulates the value usually varies between 10 and 0.1 (van Dyne *et al.*, 1980). The forage ratio (*FR*) is widely considered to be a reliable measure of preference when exploitation is not significant (Crawley, 1983), and is the basis from which most other commonly used preference indices are derived (reviewed by Lechowicz, 1982). The *FPI* differs from the *FR*, however, in two important respects. The *FPI* is based on usage and availability data that were collected (1) concurrently and (2) along the same foraging path. In contrast the *FR* compares proportional usage of a food component with proportional "availability" of that component in the environment

(i.e. a vegetation community). This entails separate sampling of usage and availability at different times over different areas, leading to sampling errors (Owen-Smith and Cooper, 1987a). Also, phenological variation within the food resource is not easily accounted for. The measurement of proportional occurrence of food components (in this case plant species) along the foraging path removes sampling error in estimating availability, and linked sampling of usage and availability ensures concurrent tracking of phenology.

A drawback to the *FPI* (and *FR*) is that the value of this index varies asymmetrically from zero towards infinity. This can be rectified by log-transformation, although the range of *FPI* values still varies as a function of relative abundance. For this reason *FPI* values can only be compared between herbivore species when the relative abundance of available food types is similar for each (Jacobs, 1984). This limits quantitative comparisons to situations where syntopic herbivore species were studied concurrently. Alternatively rank order comparisons may be more appropriate (Johnson, 1980). Despite its shortcomings, the simple usage/availability ratio yields very similar results to other more complex electivity indices (Lechowicz, 1982). Note though that only usage and availability of woody plants is considered in this analysis. If forbs and grasses were included then woody

plants, now being relatively less "available", would score higher *FPI* ratings (see also Johnson, 1980; Owen-Smith and Cooper, 1987*a*).

The *FPI* is similar in principle to the site-based acceptance (*SA*) index of Owen-Smith and Cooper (1987*a*) in that both indices are derived from measurements of usage and availability along the foraging path. The availability component of the *SA* is derived by recording relative frequency of occurrence of plant species within 10 m on either side of the foraging path during 30-minute intervals. This sampling method is not suitable for monitoring wild animals from a vehicle, however, and in this situation "snapshot" availability sampling over a smaller area is more applicable. The large sample sizes obtained by this method compensate for the small area sampled each time (the number of availability samples recorded for giraffe, kudu, impala, and steenbok were 822, 813, 169, and 151 respectively). An added advantage of the *FPI* is that availability was only recorded when the focal animal was actually feeding, providing an accurate reflection of the animal's feeding choice. To accomodate for seasonal variations in feeding preference, *FPI* values were calculated separately for wet and dry seasons. For each species, usage/availability data were collected for as large a sample of animals as possible, and in the case of kudu, from a range of social groupings.

This minimized the influence of individual or group preference on the patterns of feeding preference ascribed to each species (see Provenza and Balph, 1988).

4.2.10 Feeding preference similarities

Lawlor (1980) proposes the following formulation (adapted from Schoener, 1974*b*) for estimating similarity (S_{jk}) between the resource use patterns of syntopic consumer species j and k:

$$S_{jk} = \frac{\Sigma\ a_{ij}\ a_{ik}}{\sqrt{(\Sigma\ a_{ij}^2\ \Sigma\ a_{ik}^2)}}$$

where a_{ij} and a_{ik} are electivities (of consumers j and k respectively) for the ith resource type. This formulation is identical to that for the Pearson product-moment correlation coefficient r (see Zar, 1984). Hence by substituting log *FPI* for a and r for S_{jk}, simple linear correlation analysis was used to assess similarities between species pairs in terms of woody plant feedi preferences, during wet and dry seasons. The SAS CORR procedure was used (SAS Institute Inc., 1985*a*).

4.2.11 Plant chemistry

Plant chemical analysis was initially not planned for inclusion in this study. However, an opportunity arose during the early stages of fieldwork for a limited number of leaf samples to be analysed at the Institute of Arctic Biology, University of Alaska. At this stage feeding preferences had not yet been determined for the study animals, so 7 common species of woody plant were chosen at random, as well as 5 species of herbaceous dicot (including one creeper).

i. Sampling

Leaves were plucked at random from at least 10 plants of each species at various locations within the study area during January (mid- wet season). At this time leaves are mostly mature, but some new *Acacia nigrescens* leaves were also collected and analysed separately from mature leaves. Pooled leaf samples from each species were air-dried in paper bags hanging in the shade, and then milled and stored at low temperature until analysed in the USA.

ii. Assays

Leaf samples were analysed for condensed tannins (proanthocyanidins), total phenolic substances,

nitrogen, and phosphorus according to the methods of Bryant *et al* (1985). Condensed tannins were quantified by the proanthocyanidin assay using a hot butanol-HCl extraction, with a quebracho tannin standard. Total phenolic substances were quantified by the Folin-Denis assay with a tannic acid standard (Martin and Martin, 1982). In both cases absorbance was measured using a Perkin-Elmer Lambda 1 spectrophotometer. Leaf nitrogen and phosphorus were analysed on a Technicon autoanalyser using a sulphuric/selenious acid digest and colorimetric assay with a ferricyanide blue reaction for nitrogen and a molybdate blue reaction for phosphorus. In each leaf chemistry assay, five replicate samples were analysed for each plant species.

iii. Simple linear correlation analyses

Firstly, leaf chemistry levels in the seven woody plants assayed were compared with feeding preference values (log *FPI*) during wet and dry seasons, as detected for each of the four browser species. Pearson's product-moment method of correlation analysis was used. Secondly, for each leaf chemical factor assayed, woody plants were ranked in order of concentration level and herbaceous plants were given one combined ranking. These rankings were compared with rankings assigned to the same set of plants for relative dietary importance (as measured in terms of

feeding time allocation) during wet and dry seasons for each of the four browser species. Spearman's rank correlation method was used. Correlation analyses were performed using the SAS CORR procedure (SAS Institute Inc., 1985*a*).

In both sets of analyses, some correlations were performed using combined data sets for kudu, impala and steenbok. In each case the combined data set was derived by concatenation of the three smaller data sets. That is, observations in each variable did not change in value by being combined as data sets were simply aligned one below the other [the SAS SET (concatenate) statement was used: SAS Institute Inc., *1985a*].

iv. Partial correlation analysis

To remove the effects of interactions between leaf chemistry variables, partial correlation coefficients were calculated for feeding preference (log *FPI*, the dependent variable) and each leaf chemistry variable in turn (i.e. holding all others constant in each case). This analysis was performed for a combined kudu/impala/steenbok data set (reasons are apparent in the results section). The SAS REG procedure was used (SAS Institute Inc., 1985*b*).

4.2.12 Feeding height

Mean feeding height above ground was calculated for each browser during each month of the year using the four height classes corresponding to neck angles (subtended by the neck relative to the forelegs) of 45°, 90°, 135°, and 180° respectively (Table 4.1). Mean feeding height during each month was calculated for each browser species as follows:

$$\text{Mean height} = \Sigma\ p_i\ h_i,$$

where p_i is the proportion of feeding time allocated to feeding in the ith neck angle class, and h_i is the mean height above ground (in metres) of the ith neck angle class for the browser species in question.

4.3 RESULTS

4.3.1 Diet composition

i. Giraffe

The mean annual giraffe diet was almost entirely derived from woody plants (99.1% feeding time, Fig. 4.1), and the small herbaceous fraction consisted of creepers growing within the woody layer. Foliage made up the bulk of the woody dietary component, with only four plant species accounting for 95% of this. These were *Acacia nigrescens*, *A. tortilis*, *Dichrostachys cinerea*, and *A. exuvialis* (Appendix B1). Reproductive parts of woody plants contributed significantly to the dry season diet, with pods being particularly important in the early dry season, and flowers in the late dry season (Fig. 4.2a). Pods of *A. tortilis* and *D. cinerea* made a very large contribution to the diet in April (24% feeding time), and in June *A. tortilis* and *D. cinerea* pods together accounted for 24.9% (15.5% and 9.4% respectively) of the feeding time for that month. In September *A. nigrescens* trees flower in profusion in the KNP, and at this time the giraffe diet included a high proportion of these flowers (18.6% feeding time). Osteophagia was commonly observed during both wet and dry seasons.

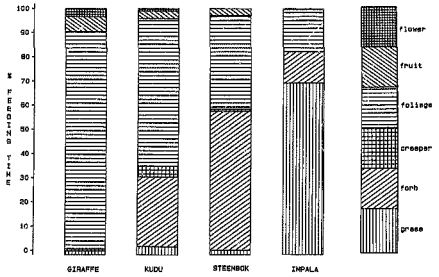
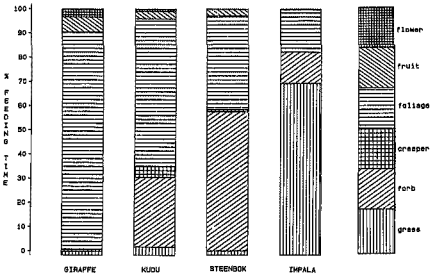


Figure 4.1. Percentage allocation of feeding time by each browser species to each of the major dietary components, averaged over the seasonal cycle. Note that "flower", "fruit", and "foliage" constitute the woody browse component.



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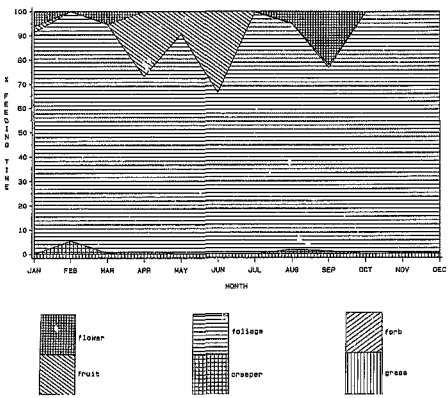

Figure 4.2a. Giraffe monthly diet composition, as measured in terms of percentage allocation of feeding time to each major dietary component. Refer to Appendix B1 for a break-down by forage types.

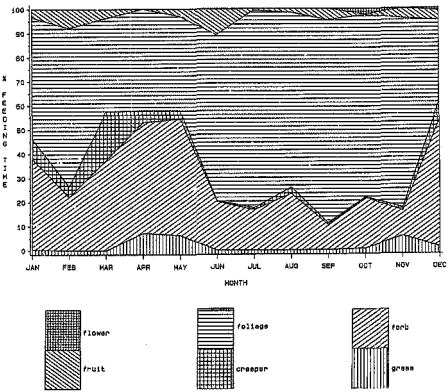

Figure 4.2b. Kudu monthly diet composition, as measured in terms of percentage allocation of feeding time to each major dietary component. Refer to Appendix B2 for a break-down by forage types.

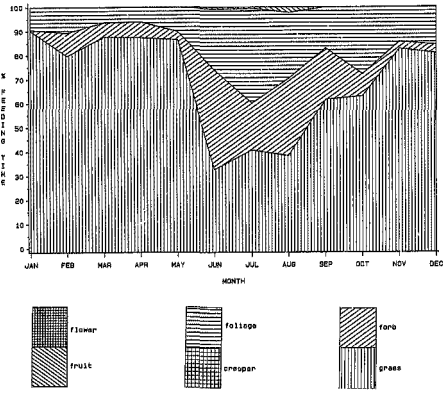

Figure 4.2a. Impala monthly diet composition, as measured in terms of percentage allocation of feeding time to each major dietary component. Refer to Appendix B3 for a break-down by forage types.

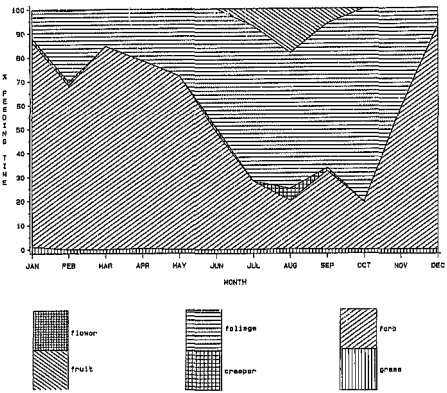

Figure 4.2d. Steenbok monthly diet composition, as measured in terms of percentage allocation of feeding time to each major dietary component. Refer to Appendix B4 for a break-down by forage types.

ii. Kudu

The mean annual kudu diet differed from that of giraffe by the inclusion of a large herbaceous component (35.1% feeding time), consisting mainly of forbs (Fig. 4.1). This herbaceous component declined markedly in the late wet season, which kudu compensated for by spending more time feeding on woody browse (Fig. 4.2*b*). The small grass component (1.7% feeding time) was included in the diet only when fresh green shoots emerged shortly after good rains. Creepers were consumed throughout the year, but were most prominent in the diet during the late wet season (20.1% feeding time for March). The creepers consumed by kudu were mainly those species growing within the herbaceous layer such as *Ipomoea obscura*, *Cucumis anguria*, and *Turbina oblongata* which intertwine among grass tufts. The large woody component of the kudu diet consisted mainly of foliage (60.9% mean annual feeding time) of which, like giraffe, *Acacia nigrescens* and *Dichrostachys cinerea* were prominent (Appendix B2). The deciduous shrub *Securinega virosa*, although relatively insignificant in the giraffe diet, was an important food plant for kudu in the wet season (26.2% feeding time for February). Kudu spent less time feeding on the reproductive parts of woody plants compared to giraffe, but these were nevertheless consumed throughout the year. In the late wet season

fallen fruits (drupes) of *Sclerocarya birrea* were sought out and avidly consumed (accounting for 7.7% feeding time for February), and in the early dry season *D. cinerea* pods were eaten off the plant (10.6% feeding time for June). Kudu allocated less feeding time to the late dry season bloom of *A. nigrescens* flowers (3.4% feeding time for September) than did giraffe. Although [illegible] during feeding observations, kudu (usually [illegible] riverine vegetation were seen feeding on the large and fleshy flowers of *Kigelia africana*, which drop to the ground in the late dry season (September). In the early wet season kudu were attracted to the fruits (drupes) of *Ximenia caffra*, which were eaten off the plant (2.9% feeding time for November).

iii. Impala

On a mean annual basis, impala allocated more feeding time to grazing (89.2%) than browsing (Fig. 4.1). The grass component in the diet varied considerably between wet and dry seasons, however, ranging from 90.2% feeding time in January to 82.6% in June (Fig. 4.2c). The dry season reduction in grass consumption was compensated for by an increased intake of browse, both herbaceous and woody. Herbaceous browse in the impala diet consisted almost entirely of forbs, since creepers made a negligible contribution. Unlike kudu and steenbok, the proportion of feeding time allocated to

forbs increased in the dry season as impala ate the dead and dried tissue of dormant forbs such as *Cryptocarpa angustifolia*, which kudu and steenbok ignored. The woody component of the impala diet was derived mainly from the foliage of *Acacia tortilis*, *A. nigrescens*, and *Dichrostachys cinerea* (Appendix B3). Fallen pods of *A. tortilis* made a small contribution to the late dry season diet (2.4% feeding time for August). The consumption of flowers by impala was not recorded during feeding observations, although they were seen eating the fallen flowers of *Kigelia africana* in riverine vegetation during the dry season.

iv. Steenbok

The large herbaceous component (58.5% feeding time) in the mean annual diet (Fig. 4.1) was derived almost entirely from forbs, with grass and creepers being relatively unimportant (both < 1% feeding time). As with kudu, the proportional allocation of feeding time to forbs declined markedly through the dry season (from 92.5% in December to 19.5% in October, Fig. 4.2d). The small creeper component in the diet was highest in the dry season (4.8% feeding time for August) during which wild cucumbers (Cucurbitaceae) retained some green foliage. The increased consumption of woody foliage which compensated for the decline in forb availability during the dry season was derived mainly from

Securinega virosa, *Acacia tortilis*, and *A. nigrescens* (Appendix B4). *S. virosa* was a particularly important food plant for steenbok in the early dry season (40.8% feeding time for June) before leaf abscission in July/August. Dried *A. tortilis* pods were searched for (apparently by smell) and eaten off the ground in the late dry season, accounting for a relatively large proportion of feeding time during this period (18.3% feeding time for August). Steenbok were not seen to consume any flowers of woody plants, although the flowers of various forbs were consumed together with leaf and stem tissue during the wet season.

4.3.2 Seasonality

4.3.2.1 *Diet composition*

i. Grass

Over all months during which data were collected, it was only with impala that monthly percentage dietary contribution of grass was significantly correlated with rainfall (Table 4.3). For impala the strongest relationship was with the 2-MRMR (see also Fig. 4.3), demonstrating the lag period between rainfall and its ultimate effects on the ungulate diet. By plotting the impala monthly percentage allocation of feeding time to grass (y) against the 2-MRMR (x), a threshold effect

Table 4.3. Correlation coefficients[1] for the relationship between (a) proportional feeding time allocation to grass and (b) rainfall figures.

Species[2]	Values of r for grass consumption vs rainfall figures[3]							
	Complete study period				1986 only			
	Monthly	2-MRMR	3-MRMR	4-MRMR	Monthly	2-MRMR	3-MRMR	4-MRMR
Kudu	-0.06	0.16	0.17	0.12	0.13	0.58[*]	0.56[*]	0.39
Impala	0.30	0.56[*]	0.62[*]	0.56[*]	0.49	0.82[**]	0.73[*]	0.68[*]
Steenbok	0.03	0.29	0.38	0.60	0.01	0.25	0.34	0.48

[1] Pearson's product-moment correlation coefficient (r). For complete study period $n = 21$ for kudu, $n = 17$ for impala, $n = 13$ for steenbok. During 1986 $n = 12$ in all cases.
[2] Giraffe excluded as this species was never observed feeding on grass.
[3] Rainfall figures (mm): Monthly, monthly total; 2-MRMR, 2-month running mean of rainfall; 3-MRMR, 3-month running mean of rainfall; 4-MRMR, 4-month running mean of rainfall.
[*] $P \leq 0.05$
[**] $P < 0.005$

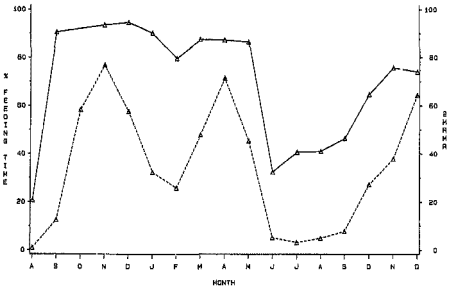

Figure 4.3. Impala percentage feeding time allocation to grass, plotted for each month from August 1985 to December 1986 (solid line), with the 2-month running mean of rainfall (2-MRMR, dashed line) in mm.

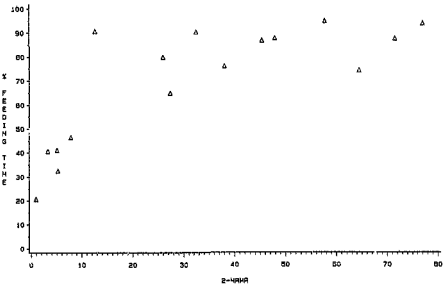

Figure 4.4. Impala percentage feeding time allocation to grass, plotted against the 2-month running mean of rainfall (2-MRMR, in mm). Note that grass consumption only starts to decline after the 2-MRMR has fallen below ± 30 mm.

becomes apparent (Fig. 4.4). Grass consumption remained constantly high at a mean of about 86% feeding time, as long as the 2-MRMR exceeded approximately 30 mm. Below this threshold level, green grass leaf availability was probably moisture limited and proportional grass consumption varied closely with the 2-MRMR (r = 0.93, P < 0.01, n = 8).

Grass consumption contributed only a very small percentage (< 2%) to the kudu mean annual diet (Fig. 4.1, Appendix 1) but this was concentrated in feeding bouts when grass shoots emerged after good rains. 72% of days on which kudu were observed grazing were within at least 5 days of the last rainfall event. *These grazing bouts accounted for 88% of all kudu* grazing time recorded. Kudu monthly proportional allocation of feeding time to grass was significantly correlated with rainfall (2-MRMR and 3-MRMR) only during the relatively dry year of 1986 (Table 4.3).

Grass was not eaten by giraffe and was insignificant in the steenbok diet, so seasonality in grass quality did not influence the feeding patterns of these species.

ii. Forbs

Over the complete study period there was no significant relationship between kudu monthly proportional forb

consumption and rainfall (Table 4.4). A very strong relationship was found to apply, however, during the drier year of 1986. The lag effect (see above) is evident in that rainfall figures most closely related to monthly kudu forb consumption were the 2-MRMR and 3-MRMR. The weaker relationship with monthly rainfall was not significant.

The lack of a relationship between kudu monthly forb consumption and rainfall during the first half of the study period (Fig. 4.5) can be explained in terms of the amount of rain received. During the 1984/85 wet season (July to June) 809 mm fell in the study area, but only 439 mm fell in the following 1985/86 wet season. The very wet spell in early 1985 would have raised the soil moisture content to a level such that forbs were probably not water limited, and so the proportional representation of forbs in the kudu diet was not limited by forb availability. From Fig. 4.5 it is clear that the total amount of rain received during the wet season has a profound effect on kudu forb consumption in the following dry season. After the good rains in the 1984/85 wet season, allocation of kudu feeding time to forbs first fell below 10% in October 1985 (end of the dry season). After the poor wet season of 1985/86, the 10% level was reached as early as June 1986 (early dry season).

Table 4.4. Correlation coefficients[1] for the relationship between (a) proportional feeding time allocation to forbs and (b) rainfall figures.

Species[2]	Values of r for forb consumption vs rainfall figures[3]							
	Complete study period				1986 only			
	Monthly	2-MRMT	3-MRMR	4-MRMR	Monthly	2-MRMR	3-MRMR	4-MRMR
Kudu	0.04	0.17	0.23	0.32	0.60	0.86[**]	0.82[**]	0.85[*]
Impala	-0.57[*]	-0.72[**]	-0.62[*]	-0.54[*]	-0.48	-0.78[**]	-0.69[*]	-0.55
Steenbok	0.55[*]	0.81[**]	0.68[**]	0.66[**]	0.53	0.73[**]	0.67[**]	0.66[**]

[1] Pearson's product-moment correlation coefficient (r). For complete study period $n = 25$ for kudu, $n = 17$ for impala, $n = 13$ for steenbok. During 1986 $n = 13$ in all cases.
[2] Giraffe excluded as forbs were insignificant in the diet of this species.
[3] Rainfall figures (mm): Monthly, monthly total; 2-MRMR, 2-month running mean of rainfall; 3-MRMR, 3-month running mean of rainfall; 4-MRMR, 4-month running mean of rainfall.
[*] $P \leq 0.05$
[**] $P < 0.005$

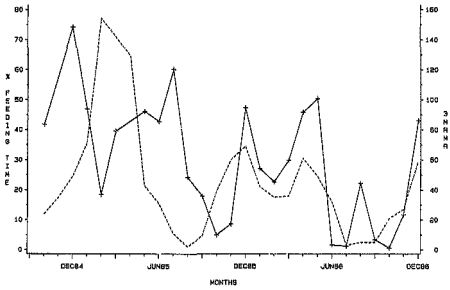

Figure 4.5. Kudu monthly percentage feeding time allocation to forbs (solid line), plotted for each month during the study period with the 3-month running mean of rainfall (3-MRMR, dashed) in mm.

In the case of impala, monthly forb consumption was negatively related to rainfall (Table 4.4), in contrast with the positive relationships that applied to kudu and steenbok (see below). This is a reflection of the secondary importance (after green grass leaf) of forbs to impala as a forage type, with impala only increasing their forb intake when green grass availability is low in the dry season. The the relationship between impala forb consumption and rainfall is best described by a curve (Fig. 4.6). Proportional forb consumption only began to increase significantly after the 2-MRMR had dropped below a threshold level of approximately 30 mm.

In the case of steenbok, seasonal variation in proportional allocation of feeding time to forbs was very closely linked to seasonal variation in rainfall, and hence forb availability (Table 4.4, Fig. 4.7). This, and the fact that steenbok were found to allocate over 90% of their feeding time to forbs in the mid- wet season (Appendix B4), demonstrates the prime importance of forbs to the diet of steenbok in the central KNP. Steenbok feeding data were not collected during the first (wetter) half of the study period. Hence it was not possible to tell if the strong relationship between steenbok forb consumption and rainfall falls away (as with kudu) once recent rainfall has exceeded a certain threshold level. This is highly probable though, considering the importance of the rainfall threshold

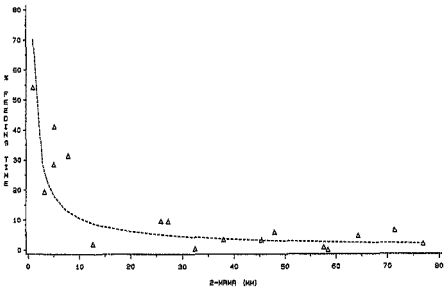

Figure 4.6. Impala monthly percentage feeding time allocation to forbs, plotted against the 2-month running mean of rainfall (2-MRMR, in mm). Note how forb consumption increases below ± 30 mm. $y = 64.56x^{-0.75}$, $r^2 = 0.53$, $P < 0.001$.

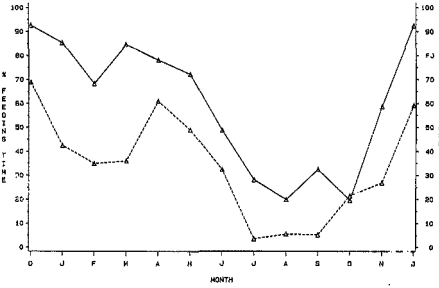

Figure v.7. Steenbok monthly percentage feeding time allocation to forbs (solid line), plotted for each month from December 1985 to December 1986 with the 3-month running mean of rainfall (3-MRMR, dashed) in mm.

effect to diet composition in kudu and impala.

iii. Creepers

For all four browsers, monthly proportional allocation of feeding time to creepers (a relatively minor dietary component in all cases, see Fig. 4.2a-d) was not found to vary significantly with the seasonal rainfall cycle.

iv. Foliage of woody plants

For those browsers that feed in the herb layer as well as the woody layer (i.e. kudu, impala and steenbok), it is to be expected that the monthly proportion of feeding time allocated to woody browse would vary seasonally. This is simply in consequence of seasonal variation in the monthly proportion of feeding time allocated to herbaceous forage types. For giraffe, which fed almost exclusively on woody browse throughout the year, no clear seasonal patterns were evident in the use of foliage on "staple" woody browse species (e.g. *Acacia nigrescens*, see Appendix B1).

v. Fruits and flowers of woody plants

These were consumed to a greater or lesser degree throughout the year (Fig. 4.8). With regard to the use of fruits, the main seasonal pattern was the

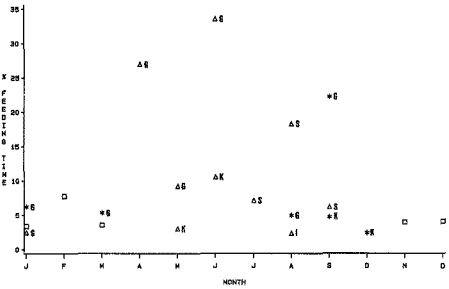

Figure 4.8. Percentage monthly feeding time allocated to the fruits and flowers of woody plants by giraffe (G), kudu (K), impala (I) and steenbok (S). Triangles denote pods, stars denote flowers, and squares denote drupes and berries (in this case consumed by kudu only). Note that pods are a particularly important food resource in the dry season (April-September). See Appendix B for a breakdown by plant species.

distinction between pods (of various *Acacia* spp and *Dichrostachys cinerea*), which were eaten in the dry season by all four browsers (off the tree by giraffe and kudu, off the ground by impala and steenbok), and fleshy drupes and berries (e.g. *Sclerocarya birrea*, *Ximenia caffra* and *Securinega virosa*) that were eaten in the wet season (mostly by kudu). Flowers were consumed mainly by giraffe, but also kudu (flowers of woody plants are usually inaccessible to impala and steenbok), during both wet and dry seasons (Fig. 4.8).

4.3.2.2 *Movement across the catenary drainage sequence*

i. Giraffe

Use of habitats of the lower catena (watercourse and riverine vegetation) began to increase in the dry season when the 4-MRMR fell below approximately 65 mm, and rose sharply when it fell below 20 mm (Fig. 4.9). When recent rainfall had been high, no use was made of these habitats. Between the 4-MRMR levels of 20 mm and aproximately 60 mm, use of the lower catena was either relatively high (± 25% of monthly sightings) or not at all (0%). This dichotomy can be explained by the tendency for giraffe to be attracted to the upper catena when *A. tortilis* and *Dichrostachys cinerea* are in pod in the early dry season, and particularly when *A. nigrescens* is in flower in the late dry season. In

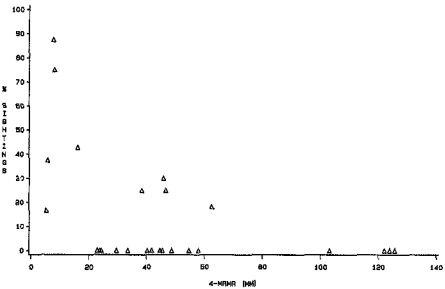

Figure 4.9. Sightings of collared giraffe in riverine and watercourse habitats during each month (as a percentage of the total sightings over all habitats for each month in question), plotted against the 4-month running mean of rainfall (4-MRMR) for each month over the complete study period.

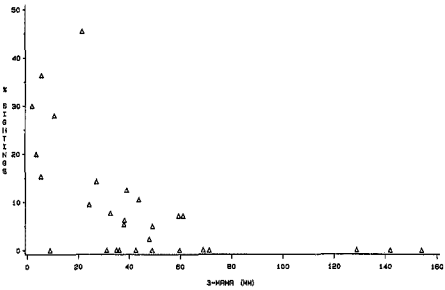

Figure 4.10. Sightings of collared kudu in riverine and watercourse habitats during each month (as a percentage of the total sightings over all habitats for each month in question), plotted against the 3-month running mean of rainfall (3-MRMR) for each month over the complete study period.

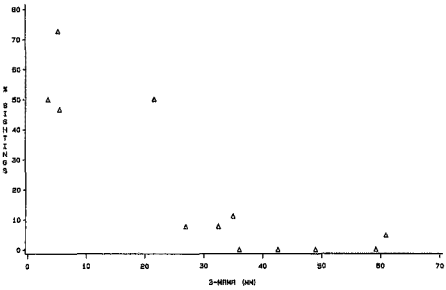

Figure 4.11. Sightings of collared impala in riverine habitat during each month (as a percentage of the total sightings over all habitats for each month in question), plotted against the 3-month running mean of rainfall (3-MRMR) for each month that impala were studied.

between these fruiting and flowering events, giraffe were attracted to the lower catena by the availability of green woody browse.

ii. Kudu

The monthly percentage of marked kudu located in riverine and watercourse habitats increased sharply when the 3-MRMR fell below approximately 36 mm (Fig. 4.10). Above this level, little or no use was made of these habitats.

iii. Impala

The same threshold effect as with kudu was apparent with impala in that as long as the 3-MRMR exceeded approximately 36 mm, impala spent little or no time in riverine vegetation (Fig. 4.11), keeping to the *Acacia* savannas of the upper catena. Below this threshold (which came into effect in May/June), use of the riverine habitat increased significantly.

iv. Steenbok

No seasonal movement across the drainage catena was detected for steenbok.

4.3.3 Dietary overlap

i. Percentage similarity (*PS*)

For all pairs excepting kudu/steenbok, *PS* increased from the late wet season through to the late dry season, and then declined again in the early wet season (Table 4.5). *PS* for the kudu/steenbok comparison was consistently high throughout the year, showing little seasonal variation. A comparison of mean annual *PS* values shows that the kudu/steenbok pair had the greatest dietary overlap, and giraffe/impala the least. In terms of mean *PS* per species kudu was the highest (40%), followed by steenbok (36%), giraffe (29%), and impala (23%).

ii. Correlation analyses

Of the correlation analyses performed over all forage types (Table 4.6a), the diets of kudu and steenbok were strongly positively correlated throughout the year, and the diets of giraffe and kudu were strongly positively correlated during the late dry and early wet seasons (3rd and 4th quarters). No significant correlations were found for any of the other diet pairs. The quarterly multiple correlation coefficient (R) values reflected the same pattern as the mean quarterly *PS* values by increasing from the late wet season through

Table 4.5. Quarterly *PS* values for diet composition comparisons per species pair.

Quarter[1]	*PS* value per species pair[2]						Mean
	G/K	G/I	G/S	K/I	K/S	I/S	
1/4	26.6	7.7	6.2	9.8	47.6	11.6	18.2
2/4	34.3	13	11.2	28.4	50.9	23.5	26.9
3/4	50.5	20.2	35.1	31.4	48.3	46.6	38.7
4/4	46.2	13.3	25.6	18.7	52.4	21.5	29.6
Mean	42.4	16.6	26.6	24.2	53.4	27.6	

[1] 1/4, January-March; 2/4, April-June; 3/4, July-September; 4/4, October-December.
[2] G, giraffe; K, kudu; I, impala; S, steenbok

Table 4.8a-c. Quarterly correlation coefficients[1] for diet composition comparisons per species pair.

Quarter[2]	Value of r per species pair[3]						R	
	G/K	G/I	G/S	K/I	K/S	I/S		
1/4	0.21	-0.02	-0.05	-0.00	0.87**	0.02	0.82	
2/4	0.25	-0.03	-0.04	0.28	0.91**	0.17	0.70	
3/4	0.76**	0.06	0.38	0.22	0.53**	0.35	0.76	Table 4.8a. All forage types (browse + grass)
4/4	0.56**	0.02	0.25	0.19	0.89**	0.04	0.69	
Mean[4]	0.47**	0.21	0.10	0.16	0.86**	0.13	0.69	
1/4	0.21	0.47**	-0.05	0.69**	0.87**	0.76**	0.77	
2/4	0.25	0.17	-0.05	0.89**	0.91**	0.69**	0.82	
3/4	0.76**	0.22	0.38	0.54**	0.63**	0.67**	0.83	Table 4.8b. Grass excluded (browse only).
4/4	0.55**	0.52*	0.24	0.82**	0.89**	0.79**	0.82	
Mean[4]	0.47**	0.31	0.10	0.79**	0.88**	0.90**	0.83	
1/4	0.46**	0.60**	0.11	0.23	0.61**	0.22	0.76	
2/4	0.75**	0.61**	0.12	0.27	0.37	0.14	0.69	
3/4	0.87**	0.68**	0.61**	0.34*	0.56*	0.74**	0.86	Table 4.8c. All herbs excluded (woody browse only).
4/4	0.69**	0.60**	0.76**	0.80**	0.70**	0.90**	0.90	
Mean[4]	0.84**	0.66**	0.66**	0.38*	0.67**	0.67**	0.86	

[1] Pearson's product-moment correlation coefficient (r), and the multiple correlation coefficient (R) which indicates overall correlation between the diets of all 4 browsers. In all cases $n \geq 23$.
[2] 1/4, January-March; 2/4, April-June; 3/4, July-September; 4/4, October-December.
[3] G, giraffe; K, kudu; I, impala; S, steenbok.
[4] Correlation coefficients calculated using mean annual diet composition data for each species.
* $P < 0.05$
** $P < 0.005$

to the late dry season, and decreasing again in the early wet season. As with the mean annual *FS values*, the highest two mean annual diet correlations were for the kudu/steenbok and *giraffe/kudu* pairs.

Of the correlation analyses performed over all browse dietary components (i.e. grass excluded, Table 4.6*b*), kudu/impala, kudu/steenbok, and impala/steenbok diet pairs were strongly positively correlated throughout the year. Giraffe and impala browse components were significantly correlated during the wet season (1st and 4th quarters), and giraffe and kudu diets, unaffected by the exclusion of grass, were still strongly positively correlated during the 3rd and 4th quarters. Quarterly *R* values for the browse multiple correlations were little changed through the seasonal cycle. The mean annual diet correlation coefficients showed that in the use of herbaceous and woody browse, the annual diets of kudu, impala, and steenbok were all strongly positively correlated with each other.

When all herbaceous forage types were excluded, leaving only woody browse components (Table 4.6*c*), *giraffe/kudu* and giraffe/impala diet pairs were strongly positively correlated *throughout the year. The kudu/steenbok* diet pair was significantly correlated in the late wet, late *dry, and early* wet seasons. The giraffe/steenbok, kudu/impala, and impala/steenbok diet pairs were all

only significantly correlated during the late dry and early wet seasons. Quarterly R values for the woody browse multiple correlations were lowest in the early dry season and highest in the early wet season. Compositions of mean annual woody browse dietary components were significantly correlated for all diet pair combinations.

Multiple correlation coefficients for mean annual diets showed that the value of R was smallest when all forage types were included, and largest when only the woody browse dietary components were considered. This indicates that although browsers may differ in their proportional uses of grass, forbs, and creepers, there is a general tendency for a high representation of the same set of forage types in the woody components of their respective mean annual diets.

4.3.4 Dietary diversity

The mean annual diets of giraffe and kudu were more diverse (in terms of forage types as previously defined) than those of impala and steenbok (Fig. 4.12). Through the seasonal cycle, giraffe dietary diversity was significantly lower than that of kudu (Fig. 4.13; Wilcoxon paired-sample test, $P < 0.005$). Impala dietary

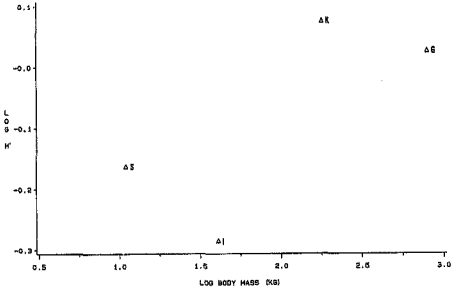

Figure 4.12. Double-logarithmic plot of diversity (H') of the mean annual diets of giraffe (G), kudu (K), impala (I) and steenbok (S), against body mass.

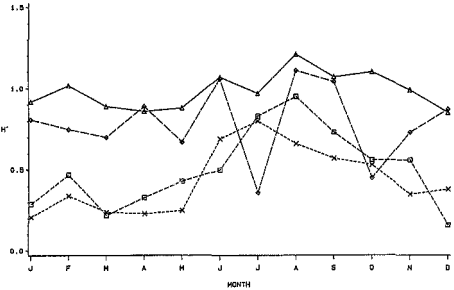

Figure 4.13. Diversity (H') of the monthly diets of giraffe (triangles), kudu (diamonds), impala (crosses) and steenbok (squares).

diversity was not significantly different to that of steenbok (Fig. 4.13).

Among kudu, impala and steenbok there was a common pattern of increased dietary diversity during the dry season, reaching a peak in July/August (Fig 4.13). No such pattern was evident in the case of giraffe. In fact the lowest value of *H'* for giraffe was during the *mid- dry season (July).*

4.3.5 Feeding preferences (Table 4.7)

i. Giraffe

In the wet season *Acacia nigrescens* scored the highest *FPI* value, followed by *A. nilotica, Spirostachys africana, A. xanthophloea,* and *Gardenia volkensii.* In the dry season a rare evergreen, *Capparis tomentosa,* was fed on for prolonged periods when encountered, resulting in a very high *FPI* value (17.3). This might have been considered an artifact caused by sampling error (to which electivity indices are prone when *availability values are very low; see* Lechowicz, 1982) if it were not that a very high *FPI* value (10.4) was also recorded for kudu feeding on the same plant during the same season. Other plant species high on the giraffe dry season preference ranking included *Spirostachys africana, Combretum mossambicense, Acacia*

Table 4.7. Feeding preference index (*FPI*) values.

Plant species[1]	Wet season[2] *FPI* values				Dry season[2] *FPI* values				Availability records[4]
	Giraffe	Kudu	Impala	Steenbok	Giraffe	Kudu	Impala	Steenbok	
Acacia tortilis	0.61	0.19	1.19	1.16	1.25	0.26	1.29	0.03	1088
Acacia nigrescens	2.62	1.46	1.59	1.14	1.39	1.52	0.79	0.76	1017
Dichrostachys cinerea	0.66	0.72	0.79	0.21	0.71	1.03	0.61	0.21	448
Securinega virosa	0.19	1.64	0.69	1.61	0.19	0.69	1.42	1.68	435
Lonchocarpus capassa	0.72	1.22	0.57	-	0.02	0.04	-	-	271
Maytenus senegalensis	0.42	0.22	1.36	0.43	0.59	0.16	0.89	0.96	159
Ziziphus mucronata	0.95	0.69	1.71	0.49	0.84	0.61	0.58	0.95	150
Acacia gerrardii	0.21	0.18	-	-	1.65	1.11	-	0.77	131
Combretum hereroense	0.63	1.65	0.29	-	0.79	2.58	0.49	-	112
Grewia monticola	0.91	0.06	0.07	-	-	0.19	1.34	-	96
Euclea divinorum	0.27	0.30	-	-	0.82	1.37	0.07	0.45	90
Acacia exuvialis	0.47	1.12	0.73	0.24	0.41	-	0.02	0.09	38
Grewia flavescens	0.91	1.65	0.20	-	0.13	1.69	0.83	-	82
Combretum imberbe	0.42	0.79	1.23	-	0.32	1.73	0.82	-	74
Ormocarpum trichocarpum	-	0.48	-	0.33	-	0.84	-	0.55	67
Ehretia amoena	0.08	0.68	0.33	0.13	-	1.26	0.33	0.65	51
Albizia harveyi	0.02	0.66	-	-	0.01	0.06	-	-	66
Dicrostachys cinerea	0.30	1.59	-	0.39	0.12	0.33	-	-	53
Maerua parvifolia	-	-	0.28	0.62	-	-	6.83	2.49	41
Peltophorum africanum	0.44	0.79	-	-	0.66	0.32	-	0.92	38
Maytenus heterophylla	0.35	0.10	0.05	-	0.11	1.33	-	-	34
Solanum panduriforme	-	0.38	-	0.02	-	1.21	-	0.06	34
Dalbergia melanoxylon	0.47	1.50	-	-	0.02	0.07	-	-	33
Acacia xanthophloea	1.29	0.29	-	-	1.67	0.70	-	-	30
Grewia bicomita	0.04	-	-	-	0.02	0.02	0.46	-	21
Ximenia americana	-	1.03	-	0.07	-	0.19	-	1.68	17
Rhus quartiniana	0.09	0.81	-	-	0.81	1.28	-	-	15
Acacia robusta	-	0.90	-	-	2.60	-	1.61	-	15
Combretum mossambicense	0.04	1.16	-	-	2.22	0.77	0.16	-	15
Combretum apiculatum	0.28	3.29	-	-	0.19	0.61	-	-	15
Gardenia volkensii	1.17	0.90	0.76	-	-	1.52	0.25	-	15
Sclerocarya birrea	0.09	1.89	-	-	0.11	1.07	-	-	14
Acacia grandicornuta	-	-	-	0.09	1.19	1.35	-	0.79	13
Cassia sobrevelata	-	-	-	-	-	2.54	-	-	12
Ximenia caffra	-	1.44	-	-	0.04	1.14	-	-	12
Commiphora schimperi	-	-	2.26	1.78	-	-	-	-	9
Lannea stuhlmannii	0.94	0.94	-	-	5.21	-	-	-	9
Acacia nilotica	2.45	1.59	-	-	0.66	0.60	-	-	8
Balanites maughamii	-	-	-	-	0.29	-	-	-	8
Ozoroa engleri	-	-	-	-	-	1.35	-	-	6
Acacia welwitschii	-	-	-	-	1.31	-	0.84	-	5
Spirostachys africana	2.23	-	-	-	2.23	-	-	-	5
Grewia microthyrsa	-	-	-	-	0.02	-	-	-	5
Combretum paniculatum	-	-	-	-	0.38	-	-	-	5
Pterocarpus rotundifolius	-	3.00	-	-	-	-	-	-	4
Protasparagus asparagoides	-	-	-	2.33	-	-	-	-	4

Continued overleaf

Table 4.7 Continued.

Plant species[1]	Wet season[2] *FPI* values				Dry season[3] *FPI* values				Availability records[4]
	Giraffe	Kudu	Impala	Steenbok	Giraffe	Kudu	Impala	Steenbok	
Strychnos spinosa	-	-	-	-	1.69	3.23	-	-	3
Solanecio speciosus	-	0.56	-	-	-	-	-	-	3
Capparis tomentosa	0.89	-	-	-	17.33	10.41	-	-	3
Dombeya rotundifolia	-	0.45	-	-	-	-	-	-	2
Phyllanthus reticulatus	-	0.30	-	-	0.92	1.11	-	-	2
Schotia brachypetalla	-	-	-	-	-	1.55	-	-	2
Croton megalobotrys	-	-	-	-	0.05	0.12	-	-	2
Albizia petersiana	-	3.71	-	-	-	-	-	-	1
Combretum zeyheri	-	-	-	-	1.31	-	-	-	1
Kigelia africana	-	-	-	-	0.10	-	-	-	1
Terminalia sericea	-	-	-	-	0.47	-	-	-	1
Cissus cirrhifolia	-	0.03	-	-	-	-	-	-	1
Cleonuepsala hildebrandtii	-	-	-	-	-	0.67	-	-	1
Gossypium herbaceum	-	-	-	-	-	0.11	-	-	1
Total availability records:									4916

[1]Listed in descending order of 'commonness' in the study area, as determined from the mean proportional frequency of occurrence of each plant species in the foraging paths of all four browser species.
[2]October to March.
[3]April to September.
[4]Total number of times that each plant species was marked 'present' in a foraging path, summed for all four browsers over both seasons.

robusta, *A. nigrescens*, *A. xanthophloea*, and *Strychnos spinosa*. With the exclusion of *A. nigrescens*, the top 7 plants on the dry season preference list occur in association with riverlines and watercourses, reflecting the tendency for giraffe to converge on these relatively very thin strips of green vegetation when the surrounding savanna is mainly brown and bare. Plants that rose considerably on the dry season preference ranking (relative to the wet season) were *Acacia gerrardii*, *Euclea divinorum*, *Rhus guenzii*, *Acacia robusta* and *Combretum mossambicense*. Apart from *A. gerrardii* (which was favoured for its pods in the dry season) these are all evergreen species where growing low on the catena.

ii Kudu

Plants scoring high *FPI* values in the wet season included *Albizia petersiana*, *Combretum apiculatum*, *Pterocarpus rotundifolius*, *Sclerocarya birrea*, *Combretum hereroense*, and *Securinega virosa*. The high preferences indicated for *A. petersiana* and *P. rotundifolius* (which has particularly leathery leaves) do not appear on the preference lists for the other browsers, nor on the kudu preference list for the dry season. Both these plants occur in discrete patches which kudu usually only move through in transit, spending little time feeding. There were, however,

narrow time "windows" during the wet season when these plants put out new growth, and then the study animals moved into the patches and fed for extended periods on young leaves.

As previously described, *Capparis tomentosa* was rarely encountered and scored a very high *FPI* value in the dry season. Other plants high on the dry season preference ranking included *Lannea stuhlmannii*, *Strychnos spinosa*, *Combretum hereroense*, and *Cassia abbreviata*.

Plants for which *FPI* values were high in the wet season and low in the dry season included *Securinega virosa*, *Lonchocarpus capassa* and *Diospyros mespiliformis*. These are deciduous species, and the leaves that remain through the dry season are dry and fibrous. Plants with low wet season preference ratings but rising in preference in the dry season included *Combretum imberbe*, *Ehretia amoena*, *Maytenus heterophylla*, *Solanum panduraeforme* and *Rhus guenzii*. These species are weakly deciduous (*C. imberbe* as saplings, trees are deciduous) or evergreen.

iii. Impala

Highest on the wet season preference ranking was *Commiphora schimperi*, a deciduous spinescent shrub. Other plants with high *FPI* rankings during the wet

season were *Ziziphus mucronata*, *Acacia nigrescens*, *Maytenus senegalensis*, *Combretum imberbe* and *A. tortilis*. During the dry season the highest *FPI* value was for a low-lying evergreen shrub, *Maerua parvifolia*. Other woody food plants with high preference rankings during the dry season were *A. robusta*, *Securinega virosa*, *Grewia monticola*, and *A. tortilis*. *FPI* values for *M. parvifolia*, *G. monticola* and *G. flavescens* rose markedly in the dry season relative to the wet season.

iv. Steenbok

In the wet season the highest *FPI* value was for wild asparagus, *Protasparagus angusticladus*. This spinescent scrambler has very fine leaves but the growing shoot tips were highly favoured, although encountered fairly rarely. Other woody food plants with high *FPI* rankings in the wet season were *Commiphora schimperi*, *Securinega virosa*, *Acacia tortilis*, and *A. nigrescens*. In the dry season these were *A. gerrardii* (saplings), followed by *Maerua parvifolia*, *S. virosa*, and *Ximenia americana*. *M. parvifolia* and another evergreen, *Maytenus senegalensis* scored low *FPI* values in the wet season, but these rose markedly in the dry season. *Euclea divinorum*, a particularly sclerophyllous evergreen, was ignored in the wet season but accepted in the dry season.

4.3.5.1 *Similarities among browser species*

Correlation coefficients (Table 4.8) show that patterns of feeding preference for woody plants (indicated by log *FPI* values) were generally weakly correlated in the wet season. The only significant relationship was for the giraffe/impala pair. In the dry season however, strong relationships were found to apply for the giraffe/kudu and impala/steenbok pairs. For each of these pairs, plant species occurring in the preference lists of both browser species are sorted in descending order of mean preference (average log *FPI* value) in Table 4.9.

Comparing feeding preference patterns between wet and dry seasons for each species, no significant relationships were found to apply (Table 4.8). This reflects a seasonal change in woody plant feeding preferences.

4.3.5.2 *Feeding preference and feeding duration* (Table 4.10)

In the wet season giraffe and kudu *FPI* rankings were significantly correlated with rankings of feeding duration per woody plant feeding event (Appendix C). That is, high preference plants were fed on for longer

Table 4.8. Correlation ...icients indicating feeding preference similarities ... g species and between seasons[1]

	Giraffe	Kudu	Impala	Steenbok	
Giraffe	0.14	0.21	0.61*	0.33	
Kudu	0.92**	0.16	-0.01	0.23	
Impala	0.00	-0.37	-0.27	0.52	Wet season
Steenbok	0.37	-0.01	0.85**	0.23	
	Dry season				

[1]Coefficients on the diagonal (underlined) are for the relationship between wet and dry seasons for the same species.
*$P < 0.05$
**$P < 0.005$

Table 4.9. Combined preference rankings for the dry season

Giraffe and kudu			Impala and steenbok		
Plant species[1]	Growth form[2]	Availability records[3]	Plant species	Growth form	Availability records
Capparis tomentosa	S/C	3	*Maerua parvifolia*	S	3
Strychnos spinosa	T	6	*Securinega virosa*	S	93
Acacia nigrescens	T	481	*Acacia tortilis*	T	145
Combretum hereroense	T	81	*Maytenus senegalensis*	S	5
Acacia gerrardii	T	194	*Ziziphus mucronata*	S/T	19
Combretum mossambicense	T	5	*Acacia nigrescens*	T	81
Acacia grandicornuta	T	6	*Ehretia amoena*	S	3
Acacia xanthophloea	T	38	*Dichrostachys cinerea*	S/T	49
Euclea divinorum	S/T	87	*Euclea divinorum*	S/T	5
Rhus guenzii	S/T	62	*Acacia exuvialis*	S	72
Phyllanthus reticulatus	S	3			
Dichrostachys cinerea	S/T	209			
Combretum imberbe	T	72			
Acacia tortilis	T	214			
Grewia flavescens	S	35			
Maytenus heterophylla	T	17			
Sclerocarya birrea	T	11			
Ximenia caffra	T	12			
Acacia welwitschii	T	5			
Acacia nilotica	T	8			
Peltophorum africanum	T	17			
Ziziphus mucronata	S/T	43			
Combretum apiculatum	T	16			
Securinega virosa	S	168			
Maytenus senegalensis	S	112			
Diospyros mespiliformis	T	20			
Croton megalobotrys	T	4			
Salvadora melanoxylon	T	28			
Lonchocarpus capassa	T	187			
Albizia harveyi	T	37			
Grewia bicolor	S	16			
Grewia monticola	S	23			

[1] Listed in descending order of preference (high at the top, low at the bottom).
[2] For each plant species, the usual growth form occurring in the study area: T, tree; S, shrub; S/C, shrub or climber; S/T, shrub or tree.
[3] Number of times that each plant species was marked present in *availability* sampling along the dry season foraging path, summed for both browsers in each pair.

Table 4.10. Correlation coefficients[1] for the relationship between rankings of feeding preference and feeding duration *per feeding event*.

Species	Values of r and (n)	
	Wet season	Dry season
Giraffe	0.72* (31)	0.60* (41)
Kudu	0.50* (39)	0.28 (49)
Impala	0.17 (17)	0.61* (19)
Steenbok	0.13 (16)	0.67* (16)

[1] Spearman's rank correlation coefficients.
* $P \leq 0.005$.

at each encounter than low preference plants. In the dry season significant correlations applied for giraffe, impala and steenbok.

4.3.5.3 *Evergreen/deciduous comparison*

Preferences (log *FPI*) for evergreen woody plants generally tended to be equal to or lower (but not signficantly) than for deciduous species in the wet season. In the dry season the reverse applied, with evergreens being generally more favoured (significant for giraffe only: *Student's t test*, $P < 0,05$).

4.3.6 Plant chemistry (Table 4.II)

Quantities of condensed tannin and total phenolic compounds in leaf samples are expressed as % dry mass for comparison with results of other studies. Note that this way of expressing results of tannin assays was criticised by Wisdom *et al.* (1987). They found that values of % dry mass, when read from a standard curve based on quebracho tannin, were different to values read from a standard curve based on tannin extracted from the plant species being assayed. However, Hole and Butler (*ms.*) have subsequently defended the use of a standard curve based on a known, purified, condensed tannin, rather than a crude extract of tannin from each plant species in question. In the rest of this thesis

Table 4.11. Results of leaf chemistry analyses, expressed as % dry mass.

Plant species	Growth form[1]	Condensed tannins		Total phenols		Nitrogen		Phosphorus	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Maytenus heterophylla[2]	T	25.56 ± 0.36		12.83 ± 0.20		1.24 ± 0.02		0.10 ± 0.05	
Combretum hereroense	T	13.97 ± 0.29		25.00 ± 0.46		1.13 ± 0.03		0.11 ± 0.00	
Maytenus senegalensis[2]	S	11.70 ± 0.33		4.07 ± 0.09		1.34 ± 0.03		0.13 ± 0.00	
Lonchocarpus capassa	T	8.06 ± 0.24		2.48 ± 0.05		3.99 ± 0.06		0.28 ± 0.01	
Acacia nigrescens (mature leaves)	T	6.46 ± 0.23		6.38 ± 0.14		2.64 ± 0.06		0.13 ± 0.06	
Acacia nigrescens (new leaves)	T	3.66 ± 0.33		5.31 ± 0.13		5.05 ± 0.06		0.44 ± 0.00	
Combretum imberbe	T	2.01 ± 0.08		15.05 ± 0.17		2.22 ± 0.04		0.14 ± 0.00	
Securinega virosa	S	1.44 ± 0.23		10.57 ± 0.45		3.05 ± 0.01		0.23 ± 0.00	
Acrotome hispida	F	0.99 ± 0.04		2.02 ± 0.06		3.93 ± 0.02		0.31 ± 0.01	
Heliotropium steudneri	F	0.97 ± 0.04		5.79 ± 0.16		4.48 ± 0.03		0.19 ± 0.00	
Ipomoea obscura	C	0.93 ± 0.11		6.72 ± 0.08		2.48 ± 0.04		0.34 ± 0.00	
Hibiscus praeteritus	F	0.92 ± 0.15		1.68 ± 0.01		3.56 ± 0.10		0.76 ± 0.00	
Justicia flava	F	0.43 ± 0.16		0.95 ± 0.01		3.43 ± 0.03		0.23 ± 0.00	

[1]T, tree; S, shrub; F, forb; C, creeper.
[2]Evergreens. All other woody plants are deciduous.

(i.e. apart from in Table 4.11) I avoid this problem of quantifying leaf condensed tannin concentration, by using the absorbance value (A_{550}) obtained in the proanthocyanidin assay as an index of condensed tannin concentration.

Obvious in Table 4.11 are the lower concentrations of condensed tannins and total phenolics in herbaceous species compared to woody species (Student's t test, one-tailed, $P < 0.05$). This result is consistent with the widespread tendency for woody plants to contain higher concentrations of phenolic compounds than herbaceous plants (Rhoades and Cates, 1976). Mature *Acacia nigrescens* leaves were significantly higher in condensed tannin and total phenolics, and lower in nitrogen and phosphorus, than young leaves ($P < 0.005$ in all cases).

4.3.6.1 *Simple linear correlation analyses*

i. Feeding preference and plant chemistry (Table 4.12)

In the wet season, feeding preference (log FPI) was strongly negatively correlated with leaf condensed tannin content for kudu, impala, and steenbok. No relationship applied in the case of giraffe. In the dry season there was no significant relationship between condensed tannin content and feeding preference for any

Table 4.12. Pearson's product-moment correlation coefficients for the relationships between feeding preference (log FPI) and leaf chemistry.

Browser species	Wet season				Dry season			
	Condensed tannin	Total phenols	N	P	Condensed tannin	Total phenols	N	P
Giraffe[1]	-0.10	-0.21	0.46	0.46	-0.09	0.30	-0.15	-0.17
Kudu[2]	-0.75[a]	0.15	0.70	0.60	0.15	0.75[a]	-0.38	-0.43
Impala[2]	-0.64[b]	-0.39	0.46	0.48	-0.62	-0.65	0.38	0.55
Steenbok[3]	-0.59	0.66	0.34	0.63	-0.52	0.82	-0.12	-0.14
Combined[4]	-0.81[**]	-0.14	0.56[**]	0.54[a]	0.01	0.32	-0.17	-0.16

[a] $P < 0.05$ [**] $P < 0.005$

[1] During both seasons $n = 7$.

[2] During the wet season $n = 7$, during the dry season $n = 6$.

[3] During both seasons $n = 3$.

[4] All 4 species combined except giraffe excluded from correlations with condensed tannin. During the wet season $n = 17$ for condensed tannin otherwise $n = 24$. During the dry season $n = 15$ for condensed tannin otherwise $n = 22$.

of the four browser species.

During both wet and dry seasons there were no consistent relationships between feeding preference and leaf total phenolic content. In fact positive relationships were indicated for kudu and steenbok, while negative relationship were indicated for giraffe and impala.

In the wet season, feeding preference was positively correlated with leaf nitrogen and phosphorus for all four browsers combined, but these relationships fell away in the dry season.

ii. Diet composition and leaf chemistry (Table 4.13)

In the wet season, rankings of condensed tannin concentrations were negatively correlated with dietary contribution rankings for kudu, impala and steenbok (combined). The same general pattern applied in the dry season, with a very weak and insignificant (albeit negative) relationship in the case of giraffe.

In the wet season, there was a consistent negative relationship between dietary contribution rankings and total phenolic concentration rankings, although for giraffe this relationship was very weak and insignificant. In the dry season there was no

Table 4.13. Spearman's rank correlation coefficients for the relationships between rankings of dietary contribution and leaf chemistry.

Browser species	Wet season				Dry season			
	Condensed tannin	Total phenols	N	P	Condensed tannin	Total phenols	N	P
Giraffe[1]	0.05	-0.07	0.67	0.29	-0.04	0.20	-0.04	0.66
Kudu[1]	-0.76*	-0.43	0.81*	0.90**	-0.74*	0.05	0.43	0.84
Impala[1]	-0.52	-0.74*	0.58	0.61*	-0.71*	-0.19	0.24	0.62
Steenbuck[2]	-0.71	-0.77	0.89*	0.94**	-0.60	-0.60	0.60	0.71
Combined[3]	-0.53**	-0.52*	0.69**	0.71**	-0.60**	-0.28	0.35	0.54**

*P < 0.05 **P < 0.005
[1]n = 6 in all cases.
[2]n = 4.
[3]All 4 species combined (n = 30), except giraffe excluded from correlations with condensed tannin and total phenols (n = 22).

significant relationship for any of the four species.

Apart from for giraffe, a consistently strong and positive relationship was found to apply between dietary contribution rankings and leaf nitrogen and phosphorus rankings during the wet season. Overall, these relationships were weaker in the dry season.

4.3.6.2 *Partial correlation analysis*

As no significant relationships were found between giraffe feeding preference and any of the leaf chemistry variables during either season (Table 4.12), partial correlations were computed for kudu, impala and steenbok (combined).

This analysis showed that condensed tannin alone accounted for much of the variation in wet season feeding preference (Table 4.14, Fig. 4.14). Contributions of the other factors were not significant. No significant relationships applied in the dry season.

4.3.7 Feeding height

i. Interspecific comparisons among adult females

On a mean annual basis, giraffe allocated almost 90% of

Table 4.14. Partial correlation coefficients for the relationships between feeding preference[1] (log *FPI*) and leaf chemistry.

Leaf chemistry *variables*	Partial correlation coefficients
Condensed tannin	0.66*
Total phenols	0.03
Nitrogen	0.01
Phosphorus	0.00

[1]Wet season feeding preferences of kudu, impala and steenbok combined.
* $P = 0.006$

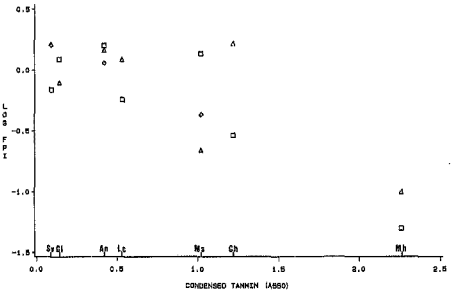

Figure 4.14. Combined plot of wet season feeding preferences (log *FPI*) of 3 browser species, against leaf condensed tannin contents (A550)* of 7 woody plant species. Browser species are kudu (triangles), impala (squares) and steenbok (diamonds). Plant species are *Securinega virosa* (Sv), *Combretum imberbe* (Cl), *Acacia nigrescens* (An), *Loxhocarpus capassa* (Lc), *Maytenus senegalensis* (Ms), *Combretum hereroense* (Ch), and *Maytenus heterophylla* (Mh).
*The absorbance value (at 550 nm) in the proanthocyanidin assay (see section 4.3.6)

feeding time to feeding above the height ranges of kudu, impala, and steenbok (Fig. 4.16). Kudu allocated 33% of their feeding time to the height range 1.2 m - 1.7 m, which was little used by giraffe and impala, and is beyond the reach of steenbok. More than half of kudu feeding time was spent feeding below this level, however. These results show that despite clear stratification in terms of mean feeding height throughout the seasonal cycle (giraffe > kudu > impala > steenbok; Fig. 4.16), there is nevertheless considerable overlap among kudu, impala, and steenbok in the use of browse at the lower feeding levels. Statistically quantifying this overlap would be trivial, as its significance for competition depends on browse biomass production within this height range, browser population densities, habitat preferences, and feeding preferences.

Among kudu, impala and steenbok, a common pattern of increased mean feeding height was evident in the dry season (see June-October, Fig. 4.16). This is a reflection of the increased use of woody browse to compensate for the reduced availability of green forage in the herb layer during this period.

ii. Giraffe cow/bull comparison (Fig. 4.17)

Mean percentage of feeding time (± S.E.) spent feeding

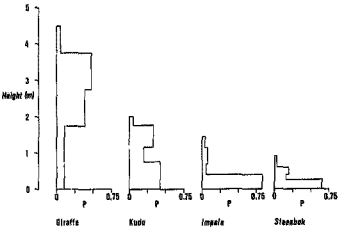

Figure 4.15. Proportions (P) of feeding time allocated to height classes, which correspond to the four neck angle classes for each browser species (see Table 4.1), calculated over the complete seasonal cycle.

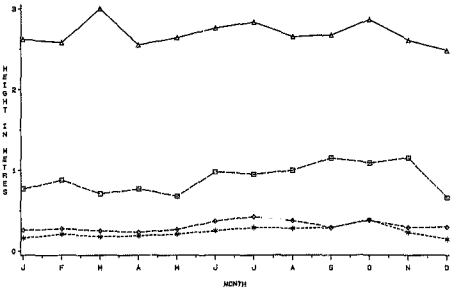

Figure 4.16. Mean feeding heights of giraffe (triangles), kudu (squares), impala (diamonds) and steenbok (stars), plotted for each month of the year.

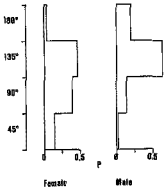

Figure 4.17. Proportion (P) of feeding time allocated to each neck angle class, by female and male giraffe respectively, over the complete seasonal cycle.

above body height (neck angle > 90°) was 49% (± 3.6%) in cows and 84% (± 4.0%) in bulls. The tendency for bulls to allocate a higher proportion of feeding time to the neck angle classes 135° and 180° held consistently through the seasonal cycle (pair-wise Student's t test, $P < 0.0005$, $n = 7$ months during which both sexes were studied, tested using arcsine-transformed data).

4.4 DISCUSSION

4.4.1 The food resource base

4.4.1.1 *Diet composition*

Results of diet composition analyses among the four ruminant species considered in this study are broadly comparable with those of single species studies conducted elsewhere in Africa.

Giraffe fed almost exclusively on woody plants, were never seen grazing, and made very little use of forbs and creepers. The same applies for giraffe in the Serengeti National Park, Tanzania (Pellew, 1984a), and the Tsavo National Park, Kenya (Leuthold and Leuthold, 1972). Only very limited use of grass was reported for giraffe in the Tarangire Game Reserve, Tanzania (Lamprey, 1963) and the Transvaal lowveld (outside the KNP), South Africa (Hall-Martin, 1974a). Giraffe have been observed grazing during the dry season in the Savuti marsh, Botswana (H. Vandewalle, personal communication), but this is unusual and probably a result of the unique situation in that area where green grass is available at a time when woody foliage is in short supply.

The very small grass component in the kudu diet was restricted to short periods following good rains. This was also the case in a previous kudu study conducted in the same area (Novellie, 1983). Kudu in the northern Transvaal were found to graze for an average of just 7% monthly feeding time, all during the wet season (Cooper, 1985; Owen-Smith and Cooper, 1985). A small amount of grass was found in the rumen contents of kudu shot in eastern Zambia during the rains (Wilson, 1965), and similar findings have been reported from Kyle and Wankie National Parks, Zimbabwe (Wilson, 1970; Conybeare, 1975).

In impala the browse/grass ratio is highly variable, depending on locality and prevailing rainfall pattern (Dunham, 1980; Smithers, 1983). In the present study however, a predominance of grass in the mean annual diet (as assessed from feeding time allocation) is in agreement with the classification of impala as an intermediate feeder preferring grass, on the basis of stomach structure (Hofmann and Stewart, 1972). Despite local variations in the mean annual browse/grass ratio in the impala diet, the pattern of increased browsing during the dry season (as recorded in this study) applies generally to impala throughout its distribution. Regions for which this pattern have been documented include the Serengeti National Park and Selous Game Reserve, Tanzania (Jarman and Sinclair,

1979; Rodgers, 1976); the Zambezi Valley and Sengwa Wildlife Research Area, Zimbabwe (Jarman, 1971; Dunham, 1980); Nylsvley Nature Reserve, South Africa (Monro, 1980; Cooper, 1985; Owen-Smith and Cooper, 1986); and the KNP, from a previous study based on rumen content analysis (Fairall, 1983).

Steenbok have been little studied with respect to diet composition, and the information available is highly variable. Smithers (1983) found equal proportions of grass and browse in a sample of rumen contents from Botswana, and in Zimbabwe 30% grass and 70% browse. Huntley (1972) found very little use of grass and a large forb component in the diet of a tame steenbok in the northern Transvaal, South Africa, which is compatible with the results of this study. From its stomach structure, Hofmann and Stewart (1972) classify the steenbok as an intermediate feeder preferring foliage of forbs, shrubs, and trees. A preference for forbs is clearly indicated by results of this study and is supported by previous observations on steenbok in the same area in the KNP (Cohen, 1976). However, the term "intermediate feeder" suggests a significant grass component in the diet which is not indicated by results presented here. A subsequent review of digestion in African wild ruminants (Hoppe, 1984) includes steenbok among the concentrate selectors, a classification well

suited by the feeding behaviour of this species in the KNP.

Giraffe, kudu and steenbok are thus clustered at one end of the grazer-to-browser continuum (*sensu* McNaughton and Georgiadis, 1986). Giraffe differ from kudu and steenbok, however, with respect to the use of (a) forbs and (b) pods and flowers of woody plants. While not used by giraffe, forbs are an important dietary component to kudu (see also Novellie, 1983; Cooper, 1985; Owen-Smith and Cooper, 1985) and particularly steenbok (see also Huntley, 1972; Cohen, 1976). Pods and flowers (mainly of the Mimosoideae) feature more prominently in the giraffe diet (see also Hall-Martin, 1974a; Pellew, 1984a) than in the diets of kudu and steenbok, to which flowers are mostly above reach and fruits (pods and drupes) are usually only accessible when they fall to the ground.

This study and others confirm that giraffe, kudu, and steenbok are almost exclusively browsers, if the term "browser" is used broadly (*sensu* Owen-Smith, 1982) to label animals that feed on dicotyledons, both herbaceous and woody (as throughout this thesis, but see Hofmann and Stewart, 1972). Impala are mixed feeders favouring green grass but including a large proportion of browse in the dry season diet. The choice of these four species to represent ruminants in the

savanna browsing guild might not be in strict accordance with Root's (1967) original guild concept. This includes only those species that exploit the *same class* of resources in a *similar way*. It is difficult to decide if, for example, giraffe and impala are trophically this similar. More recently it has been recognised, however, that the criterion for *similar way* should be based on the effect of resource use on the resource itself (Jaksic, 1981). To quote MacMahon *et al.* (1981:301), "it does not matter whether the organism removes a tree leaf for nesting material, food, or as a *substrate to grow fungi which* in turn are eaten; the leaf is gone and the leaf users belong to a common guild." By this criterion the four species included in this study are most certainly members of a common guild.

4.4.1.2 *Seasonality and diet overlap*

Below a critical threshold in the seasonal moisture cycle (about May/June), proportional use of herbaceous forage types began to decline among kudu, impala and steenbok. This was in response to the dry season decline in abundance of green forage in the herb layer (see Novellie, 1983). The result was a shift in resource use patterns within the guild, with convergence on the woody browse resource. Below a similar mid- dry season threshold, giraffe, kudu and

impala began to converge on habitats low on the catenary drainage sequence.

Such seasonal oscillations in diet composition and feeding position on the catena have now been widely documented for African savanna ungulates (Bell, 1970; Jarman, 1972; Hall-Martin, 1974b; Leuthold, 1978; Jarman and Sinclair, 1979; Pellew, 1984a; du Toit, 1987). Among the mixed species studies, the general consensus has been that the potential for interspecific competition is greatest in the late dry season when resource use patterns overlap most. However, interspecific competition hypotheses predict that the diversity of foods taken by each species in a guild should decline as food becomes less abundant, and so overlap should actually be reduced during the lean season (Smith *et al.*, 1978; Schoener, 1982, 1986a). On the other hand, if intraspecific competition prevails then dietary diversity (and hence overlap) should increase as food becomes scarce.

In the central KNP I found the diets of kudu, impala and steenbok to increase in diversity during the lean season, as did average dietary overlap. By the above theory this indicates that interspecific competition has less influence than intraspecific competition on the allocation of guild resources. Furthermore, the pattern of increasing dietary diversity and overlap

through the dry season does not support Jarman's (1971) assertion that African large herbivores (elephant, impala, kudu and buffalo were cited) each resort to distinct food staples, or "refuges" in the early dry season. *Acacia nigrescens* was the staple browse plant of both giraffe and kudu for example, and dietary overlap between kudu and impala was almost as high in the early dry season (28%) as in the late dry season (31%). It is clear, however, that riverine vegetation constitutes a dry season food "reserve" (*sensu* Hall-Martin, 1974b) for giraffe, kudu and impala (and other herbivores, both browsers and grazers). This habitat is little used in the wet season, so the common endemic food plants (e.g. *Acacia robusta* for giraffe) are probably less palatable than many of the deciduous species of the upper catena. They nevertheless sustain browsers, or at least limit condition loss, through the lean period.

4.4.2 Partitioning of the food resource base

4.4.2.1 *Differences in feeding preferences*

Apart from between giraffe and impala, indices of preference for woody plants were not correlated among browser species in the wet season. Considering that woody browse contributed only about 14% to the impala wet season diet, the giraffe/impala correlation is

hardly significant. In the dry season however, when woody browse was depended upon most, close correlations were found between feeding preferences of (a) giraffe and kudu and (b) impala and steenbok. Giraffe and kudu converged mainly in their preferences for browsing off trees such as *Acacia nigrescens*, *A. gerrardii*, *A. grandicornuta*, and *Strychnos spinosa*; and the evergreen woody climber *Capparis tomentosa*. Impala and steenbok differed from the larger pair in their mutual preferences for shrubs such as *Maerua parvifolia*, *Securinega virosa* (which scored a high *FPI* value with kudu in the wet season but not in the dry season), *Maytenus senegalensis*, and *Ziziphus mucronata* (usually a shrub in the study area).

Differences in electivities may reflect evolutionary divergence of resource use patterns, perhaps through divergence in morphological features governing resource use, due to past competitive pressures (Lawlor, 1980). Hence differences between the lean season feeding preferences of (a) giraffe and kudu, and (b) impala and steenbok indicate a low likelihood of present-day competition between these two species pairs. Separation within each pair was by steenbok remaining on the upper catena when impala moved downslope in the dry season, and by giraffe feeding at a higher level in the vegetation than kudu (section 4.4.2.3).

4.4.2.2 *Feeding preference and plant chemistry*

For the seven woody plant species assayed, wet season i .es of feeding preference among kudu, impala and steenbok were strongly negatively related with leaf condensed tannin content. Although feeding preferences were positively related to leaf nitrogen and phosphorus leve . is was because plants that were high in condensed tannin were low in nitrogen and phosphorus. The relationships between levels of these nutrients and feeding prefe.ence fell away when condensed tannin was held constant. Giraffe feeding preferences were not related to any of the leaf chemistry variables assayed, and neithe. were the dry season feeding preferences of kudu, impala and steenbok.

The strong influence of leaf condensed tannin content on wet season diet selection by kudu, impala and steenbok is consistent with previous observations and research findings on African savanna browsers (van Hoven, 1984; Cooper and Owen-Smith, 1985). Such findings conform with growing evidence that plant *secondary chemistry* is a major factor to be considered in the assessment of forage quality for browsing mammals (Freeland and Janzen, 1974; Rosenthal and Janzen, 1979; Bryant and Kuropat, 1980; Bryant *et al.*, 1985; Robbins *et al.*, 1987a). My findings do not, however, support the balance hypothesis of Cooper *et*

al. (1988). From partial correlation analysis it was clear that feeding preference was related to leaf condensed tannin content alone, and not a balance between condensed tannin and nitrogen.

It is difficult to explain why giraffe were not found to conform with the other three browser species with respect to the wet season feeding preference / condensed tannin relationship. It could be that they are less sensitive to *condensed* tannin, or alternatively that there were other overriding factors among the plant species sampled. Such factors could include plant structural features that are effective deterrents against browsing by giraffe but not the smaller species (see section 4.4.2.3). However, deactivation of dietary tannins by proline-rich salivary proteins has been demonstrated among rodents (Mehansho *et al.*, 1987), and Robbins *et al.* (1987b) found a higher content of such proteins in the saliva of deer (*Odocoileus* spp., mixed feeders) than in that of cattle and sheep (grazers). These authors also found deer saliva to be much more viscous than that of the *grazers*. Giraffe produce copious saliva which is extremely viscous (obviously more so than e.g. kudu saliva), sometimes *forming long* threads between mouth and tree (personal observations, and see Pellew, 1983b). Hence there is a good possibility that giraffe are particularly effective in deactivating tannins with

proline-rich salivary proteins, and this requires investigation.

That *feeding preferences of* kudu, impala and steenbok were not related with leaf condensed tannin levels in the dry season is to be expected. It was shown previously that dietary diversity increased among these species in the lean season (section 4.4.1.2), indicating that they were feeding on plants that would have been ignored in the wet season. That is, they were eating what they could get. Further, selection criteria could change as the leaves of some species that are favoured in the wet season (e.g. *Lonchocarpus capassa*) become dry and scabrid in the dry season. At such times the importance of leaf moisture and/or fibre content may override palatability in diet selection.

4.4.2.3 *Feeding preference and forage accessibility*

With respect to spinescence, it was found that some thornad *species, mainly Acacias, were* highly favoured as food plants by all four browser species studied. *A. tortilis* scored a consistently low preference rating with kudu, however. This plant has a combination of straight and hooked thorns, as well as very small leaves. Cooper and Owen-Smith (1986) found that kudu in the northern Transvaal were also inhibited from feeding on this species, while impala and goats were not.

Impala and steenbok in the central KNP plucked leaves between the thorns while kudu, having wider muzzles, appeared to have difficulty avoiding the straight thorns. Giraffe were less sensitive to the thorns, but mainly bit off new shoots on the upper canopy (beyond reach to kudu) on which the thorns are relatively soft (see also Pellew, 1984a). Nevertheless the giraffe preference rating for *A. tortilis* was probably elevated by its pods, which are highly favoured by a wide variety of mammals (Gwynne, 1969; Altmann *et al.*, 1987; Coe and Coe, 1987).

In contrast with *A. tortilis*, *A. nigrescens* has the largest leaflets of all African *Acacia* species (Coates Palgrave, 1981) and short recurved prickles. This species was favoured by all four browsers, was the staple food plant of giraffe, and contributed the largest proportion to the woody browse component of the kudu diet. The prickles did not appear to influence the feeding rates of kudu, impala and steenbok although individuals of all three species frequently got their ears snagged (see also Cooper and Owen-Smith, 1986). The strong, backward-pointing prickles prevented giraffe from stripping leaves off the stem, as they do with unarmed species (see also Pellew, 1984b). If it was not for the prickles the impact of giraffe herbivory on *A. nigrescens* would certainly be much more severe.

The effects of canopy characteristics on foliage acuessibility are demonstrated by *Securinega virosa*, a woody species that was virtually ignored by giraffe but highly favoured by the other browsers. This non-spinescent shrub becomes increasingly dense and twiggy in response to browsing. Similar responses by shrubs have been described elsewhere (Provenza and Malechek, 1984; Cooper and Owen-Smith, 1986). Although giraffe could bite off some shoots from lightly browsed plants they had difficulty feeding on others. Kudu were only deterred from feeding on this species in the dry season when terminal shoots tend to die back and become particularly twiggy, but impala and steenbok could insert their narrow muzzles through this outer "cage". Their preferences for this browse species, which had the lowest *leaf condensed tannin* level among the woody plants assayed, were particularly high in the dry season.

The influence of body size on forage accessibility is apparent from the dry season distinction between the woody plant feeding preferences of (a) giraffe and kudu and (b) impala and steenbok. This was by virtue of the larger pair having relatively higher preferences for certain tree species, and the smaller pair having relatively higher preferences for certain shrub species. Although giraffe and kudu had very similar

preferences for woody plants in the dry season, they were almost completely separated vertically, as giraffe nearly always fed at a higher level than kudu. Only one third of kudu feeding time was at a level between those used by giraffe and impala, however, and impala and steenbok feeding levels overlapped almost completely. Hence the assumption that browsers separate by using *different feeding* levels in the vegetation (Lamprey, 1963; Leuthold, 1978; McNaughton and Georgiadis, 1986) holds for the *larger species*, but not for those smaller than kudu. Overlap in feeding level among these species must be particularly high in *riverine habitats of the* northern KNP for example, where kudu and impala are syntopic with nyala (*Tragelaphus angasii*), bushbuck (*T. scriptus*), and suni (*Neotragus moschatus*).

Giraffe bulls fed at a significantly higher level than cows, often with the neck stretched vertically upwards, which cows seldom did. In East Africa it has been noted that bulls usually feed at full neck stretch while cows prefer feeding at body or knee height (Sinclair and Norton-Griffiths, 1979; Pellew, 1983a), and the pattern is so consistent that it has been used as a means of sexing giraffe from a distance (Pellew, 1984c). By *feeding at full stretch*, I suggest that bulls benefit by cropping [illegible]g shoots that are not available to cows or sub-adult males. This *might not be entirely* beneficial, however, as it entails adopting a

vulnerable posture. When feeding at full stretch the head is directed vertically upwards, which reduces vigilance, and the body is close up against the tree, which hampers rapid escape when alarmed (personal observations). Out of a sample of 559 adult giraffe sexed in the central KNP, I found a bull:cow ratio of 1:1.6 (c.f. 1:1.7 for the Serengeti; Pellew, 1983a). Pienaar (1969) found that out of 93 adult giraffe killed by lions over a 2-year period in the KNP, the cow:bull ratio was 1:1.8. Hence bulls are much more vulnerable to predation than are cows. This can be partly accounted for by their solitary habits when wandering between herds in search of cows in oestrus, but I suggest that feeding at full neck stretch increases their vulnerability. If there was no risk, then cows would be expected to feed at full neck stretch too, but they very seldom did (neither did kudu cows).

Clutton-Brock and Albon (1985) describe how, in sexually dimorphic large ungulate species, there is a tendency for increased mortality among adult males. They propose that skewed sex ratios could be associated with asymmetries in scramble competition which favour females. Giraffe bulls are bigger than cows (1 - 2 m taller at the shoulder; Hall-Martin, unpublished, cited by Smithers, 1983) and so have a larger food bulk requirement, but spend less time feeding (Pellew,

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